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Charles Robert Darwin

Papers on Pollination

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Tidsskr. Naturvidensk. Gc16

Om Orchideernes Befrugtning ved Insekter.

Af Charles Darwin — i Udtog ved M. T. Lange.

Darwins Lære om Arternes Oprindelse *) vil, hvor interessant og paa mange Punkter sandsynlig den end er, dog neppe i det hele kunne vinde Bifald. Men hvad enten man antager den, eller forkaster den, eller indrømmer dens Berettigelse i mange Tilfælde uden at tillægge den almindelig Gyldighed — hvad der maaskee turde komme Sandheden nærmest —; eet vil ingen kunne nægte: at den Grundighed, hvormed denne udmærkede Videnskabsmand undersøger Naturen for at begrunde sin Theori, er af overordenlig Nytte for Naturvidenskaben og kaster nyt Lys paa mange hidtil lidet ændsede Punkter af Naturens Rige. Dette er saaledes Tilfældet med Orchideernes Befrugtning og Insekternes Medvirken derved, der vel ikke tidligere var ganske ukjendt, idet allerede Sprengel 1793 og senere flere andre Naturforskere have paaviist meget derhen hørende, men som dog egenlig først har fundet en Fremstiller og Forklarer i Darwin, der med dette Forhold støtter sin Sætning, at alle Naturens Væsener stundom behøve en Krydsning af forskjellige Individer, eller at ingen stadig Selvbefrugtning af tvekjønnede Individer finder Sted i Naturen. Darwins Værk (On the various

*) See dette Tidsskr. 2. Række, 5. Bind.

Mo. Bot. Garden, 1893

contrivances by which British and foreign Orchids are fertilised by insects, and on the good effects of intercrossing. London. 1862) indeholder en Mængde omhyggelige og grundige Iagttagelser, der ere af stor Interesse for Botanikere; men hans Fremstilling af Naturens vidunderlige Sammenpasning af disse Forhold, der hvert Øieblik overraske baade ved Skjønhed og Snildhed, maa nødvendig kunne interessere alle, og det saameget mere som det selv uden botaniske Forkundskaber vil være temmelig let i Naturen at følge og selv at see meget af det, som han fremstiller. Her kan kun gives en Beskrivelse af Forholdet hos enkelte Arter, men dette skal fremstilles saa udførligt, at enhver, der ikke vil spare den Uleilighed at sætte sig ind i den forudskikkede Forklaring af Blomstens Bygning, vil kunne forstaae de meddelte Omstændigheder ved Befrugtningen og let selv eftersee dem i Naturen.

Blomsterdækket hos Orchideerne (Gjøgeblomsterne) bestaaer af 3 Bægerblade, der som oftest ere farvede, og af 3 ligeledes farvede Kronblade, af hvilke 1 i Regelen vender nedad, er større end de andre og af meget eiendommelig Form. Det er »Læben«, »Honninglæben«, som afsondrer Honningsaften, der lokker Insekterne til, og ofte bagtil forlænger sig i en længere eller kortere Spore (Honninggjemmet).

Indenfor dette Blomsterdække findes hos vore Arter kun 1 Støvdrager, og denne er sammenvoxet med Griffelen til en »Griffelstøtte«, saa at der sjeldent er mere at see af den end Støvknappen, hvori det befrugtende Sædstøv er indesluttet. Støvknappen er deelt i 2 Rum, der hos de fleste af vore Arter ere meget kjendelige og saa

langt fjernede fra hinanden, at de see ud som 2 særskilte Støvdragere. Medens Sædstøvet hos de fleste andre Planter bestaaer af fine, løst liggende Korn, hænge hos Orchideerne alle de smaa Korn i hvert Rum sammen og danne Smaaklumper eller Masser, der ofte bæres af en meget eiendommelig Stilk. Disse Smaaklumper tilsammen med Stilken kaldes *Støvmassen*.

Der skulde egenlig være 3 Grifler, men de ere heelt voxede sammen med Undtagelse af Arrene, og af disse flyde selv de to nederste ofte saa fuldstændigt sammen, at de see ud som eet; — kun disse to have Arrets sædvanlige Egenskaber og Bestemmelse, nemlig under Befrugtningen at gjennemtrænges af Støvkornenes lange, fine Rør, der føre Indholdet ned til Æggene i Frøgjemmet; — det tredie Ar derimod, der sidder øverst, er omdannet til et usædvanligt Redskab, som kaldes Snabelen og hos mange Orchideer slet ingen Lighed har med et virkeligt Ar. Den indeholder eller bestaaer af et klæbrigt Stof, og hos mange Orchideer ere Støvmasserne fastbæftede til en Deel af dens Yderhud, der bliver hængende ved dem, naar de bortføres af Insekter. Den Deel, som saaledes kan borttages, bestaaer hos de fleste af vore Arter af et lille Stykke Hud, som Darwin kalder Klæbeskiven, med et Lag eller en Klump klæbrig Materie under; men hos mange udenlandske Arter er Klæbeskiven saa stor, at dette Navn kun passer paa en Deel af den, medens den anden, paa hvis Top Støvmasserne sidde, kaldes Snabelens Fod eller Stilk.

De indenlandske Orchideer inddeler Darwin nu i 3 Grupper, af hvilke den første indbefatter de fleste af vore almindelige Arter, navnlig Slægten Orchis (Gjøgeurt). Støvmasserne hos denne Afdeling have forneden en med

Klæbeskiven sammenvoxet Stilk og Støvknappen er forbunden med Snabelen.

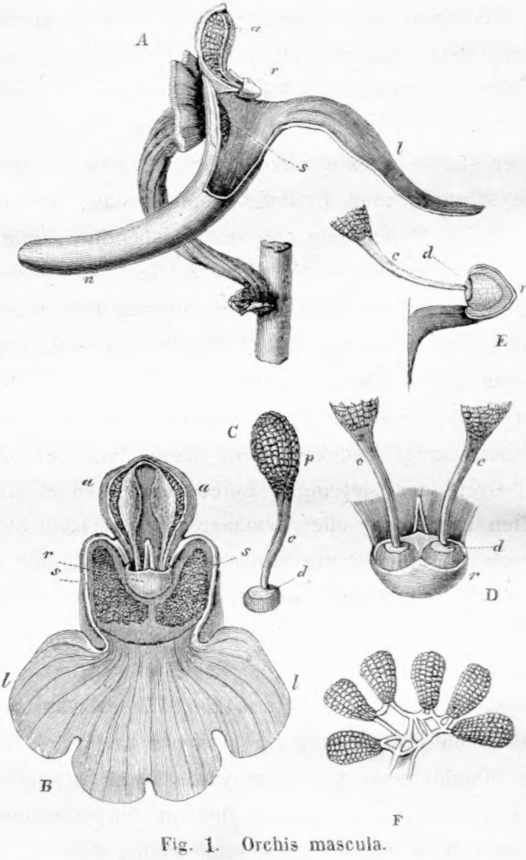

Fig. 1. Orchis mascula.

A. En Blomst seet fra Siden. Bæger- og Kronblade ere borttagne med Undtagelse af det halve af Læben og det meste af Sporen. B. Blomsten seet forfra. Alle Blade borttagne undtagen Læben. C. En Støvmasse med de smaa Pakker af Støvkorn, Stilken og Klæbeskiven. D. Snabelen seet forfra med nedtrykt Læbe. E. Gjennemsnit af Snabelen med den deraf indesluttede Klæbeskive og Støvmassens Stilk. F. Smaapakker af Støvkorn, sammenlænkede ved elastiske Traade, der i Fig. ere trukne ud fra hverandre.

a. Støvknappen. c. Støvmassens Stilk. d. Klæbeskiven. l. Læben. n. Honningsporen. p. Støvmassen. r. Snabelen. s. Arret.

Orchis mascula (tyndaxet Gjøgeurt) forekommer hyppigt hos os om Foraaret i Krat. I Fig. 1 ere Bæger- og Kronblade bortskaarne med Undtagelse af Læben med Honninggjemmet, der sees i A, n. De to Ar ere næsten sammensmeltede til eet (s), der sees under den pungformede Snabel (r). Støvknappen (A, a og B, a) vise to langt adskilte Rum, der fortil ere aabnede paalangs og hver indeholde en Støvmasse. C viser en saadan Støvmasse udtaget af sit Rum. Den bestaaer af et Antal Smaapakker af Støvkorn, der ere indbyrdes forbundne ved fine og meget elastiske Traade. I F fremstilles disse trukne ud fra hverandre. Disse Traade smelte sammen ved den nederste Ende af hver Støvmasse til en lige elastisk Stilk (C, c). Enden af Stilken hænger fast sammen med Klæbeskiven (C, d), der i E sees i Gjennemsnit paalangs, og bestaaer af et lille ovalt Stykke Hud og en Klump klæbrig Materie ved dets Underside. Enhver Støvmasse har sin særegne Klæbeskive, og de to Klumper klæbrigt Stof ligge begge indesluttede i Snabelen (D).

Denne (A, r og B, r) er næsten kuglerund, noget tilspidset og hænger ud over de to Ar. Den behøver en fuldstændig Beskrivelse, da enhver Enkelthed i dens Bygning er vigtig. E fremstiller et Gjennemsnit paalangs gjennem en af Klæbeskiverne og Klumperne, og D begge seete forfra i Snabelen, hvis forreste Læbe er trykket noget ned. Den nederste Deel af Støvknappen er forenet med Ryggen af Snabelen (B). Paa et tidligere Udviklingstrin bestaaer Snabelen af en Masse mangekantede Celler fyldte med bruun Materie, som snart opløse sig til to Klumper halvflydende, meget klæbrig og strukturløs Substans. Disse halvflydende Klumper ere noget langagtige, foroven oftest flade, forneden hvælvede. De ligge næsten frit i Snabe-

len, omgivne af Vædske og blot paa Bagsiden sammenhængende med en lille Skive af Snabelens Yderhinde, den ovenfor beskrevne Klæbeskive, der bærer Støvmassens Stilk.

Den Hud, som danner den hele ydre Overflade af Snabelen, er i Begyndelsen sammenhængende; men saasnart Blomsten aabner sig, bevirker selv den sagteste Berørelse, at den brister i en buet Tværlinie paa Forsiden, hvorved Snabelens Form ikke forandres, men dens forreste Deel bliver derved en Læbe, som let kan trækkes ned. (I B sees Randen opret, i D nedtrykt). Trykkes Læben heelt ned, saa komme de to Klumper klæbrig Materie til at ligge frit; men saasnart Trykket ophører, springer Læben op igjen paa Grund af den bagerste Deels Elasticitet og indeslutter paany de to Klumper.

Den mindste Berørelse og endogsaa Chloroformdampe bevirke denne Bristen af Huden i en bestemt Linie; maaskee brister den ogsaa undertiden af sig selv, ialtfald forberedes det ved en Svækkelse langsmed den betegnede Linie. Samtidig med at Huden brister foran, synes den ogsaa at briste bagtil i to ovale Linier, hvorved de to smaa Klæbeskiver adskilles fra Snabelens øvrige Yderflade. Da Støvknappens to Rum allerede før Blomstens Udspringning have aabnet sig fortil fra Grunden til Spidsen, saa ligge begge Støvmasserne nu, naar Snabelens Læbe trykkes ned, fuldkommen frit, men endnu paa deres Plads; nemlig Støvmasserne selv og deres Stilke i Støvknappens Rum og de smaa klæbrige Klumper, som ved Klæbeskiverne ere forbundne med dem, i Snabelens Pung.

Vi skulle nu see, hvorledes denne sammensatte Mekanisme virker. Lad os antage, at et Insekt sætter sig paa Læben af Blomsten, der frembyder en god Landings-

plads, og stikker sit Hoved ind i Kammeret, paa hvis bagerste Væg Arret (A, s og B, s) findes, for at naae ned i Honningsporen med sin Sugesnabel — eller, hvad der gjør samme Virkning, lad os skyde den fine Spids af en Blyant meget forsigtigt ind i dette Honninggjemme. Da den pungdannede Snabel rager frem i den Vei, som fører til Honninggjemmet, er det næppe muligt at føre nogen Gjenstand ind i dette uden at berøre Snabelen. Dens Yderhud vil derved briste langs med den førnævnte Linie og Læben eller Pungen let kunne trykkes ned. Naar dette er skeet, maa en af de klæbrige Klumper, eller begge, nødvendigviis komme i Berøring med det indførte Legeme og ved sin store Klæbrighed blive hængende derved. Men da denne Materie fremdeles har den Særegenhed, at den i faa Minuter tørrer ind og stivner som Kit, og da Støvknappens Rum i Forveien ere aabne fortil, saa vil en af Støvmasserne, eller begge, klæbes fast til Insektets Hoved eller Blyanten og trækkes ud med, omtrent som det fremstilles i Fig. 2 A.

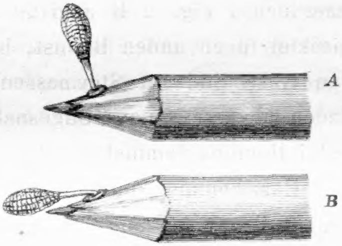

Fig. 2.
A. Støvmasssen strax efter at den har hæftet sig paa Blyanten. B. Samme efter at den har bøiet sig ned.

Det er ganske nødvendigt, at Støvmasserne klæbe sig saa fast; thi hvis de faldt ud til Siden eller tilbage, vilde de slet ikke kunne befrugte Blomsten. Efter den Stilling, hvori begge Støvmasserne sidde i deres Celle, beholde de ogsaa en lidt divergerende Retning paa det fremmede Legeme, som de nu ere hæftede til. Vedbleve de nu at

beholde denne oprette, divergerende Stilling (Fig. 2 A), vilde de igjen komme tilbage paa deres gamle Plads, hvis vi igjen førte Blyanten ind i samme eller en anden Blomsts Honninggjemme, og ingen Befrugtning finde Sted. Hvorledes bevirkes da Blomstens Befrugtning? Det skeer ved en smuk Indretning; medens nemlig den klæbrige Overflade holder fast, er den uanseelige lille Hudskive, hvorpaa Stilken sidder, udrustet med en mærkværdig Sammentrækningskraft, hvorved Støvmassen nødes til i Løbet af omtrent 30 Sekunder at bøie sig ned imod Blyantens eller Sugesnabelens Spids i en Bue af 90°, indtil den faaer den i Fig. 2 B angivne Stilling. Imidlertid flyver Insektet til en anden Blomst, hvor da, som Fig. 1 viser, den tykke Ende af Støvmassen netop maa træffe Overfladen af Arret, naar Sugesnabelen eller Blyanten føres ind i Honninggjemmet.

Her kommer nu en anden interessant Indretning, som R. Brown for lang Tid siden har beskreven, i Betragtning. Arret er meget klæbrigt, men ikke nok til at sønderrive hele Støvmassen, hvormed det nu kommer i Berøring. Det kan kun adskille de elastiske Traade, som forbinde de smaa Pakker af Støvkorn med hverandre (Fig. 1 F), og fastholde nogle af dem. Derfor kan den ene Støvmasse paa Insektets Hoved komme i Berøring med flere Ar efter hinanden og efterhaanden befrugte dem alle, saa at Insektet kun beholder Støvmassens Stilk tilbage.

Endnu et Par smaa Omstændigheder ere værd at lægge Mærke til. De smaa Klumper klæbrig Materie omgives i Snabelen af en Vædske, hvad der er vigtigt, fordi denne Materie, som sagt, tørrer meget hurtigt ind i Luften og i Løbet af faa Minuter taber Evnen til at klæbe

sig fast. Dernæst sidde de smaa Hudskiver, hvis Sammentrækning bevirker den Sænkning af Støvmasserne, der er saa nødvendig for Befrugtningen, bag i og nede i Snabelen, tæt omgivne og derved holdt fugtige af Støvknappens Basis — hvad der ogsaa er nødvendigt, da blot 30 Sekunders Udsættelse for den frie Luft er nok til at bevirke Sænkningen. Endelig er det meget vigtigt, at Læben, som forhen omtalt, igjen springer tilbage i sin forrige Stilling, naar den er bleven trykket ned. Naar et Insekt havde trykket den ned, men ikke medtaget nogen eller kun den ene af de klæbrige Klumper, vilde nemlig ellers begge Klumperne, eller den ene, som blev tilbage, udsættes for Luften og hurtigt tørre hen, saa at Støvmasserne nu bleve unyttige. Men nu er det vist, at af mange Orchidee-Arter bortføre Insekterne kun een Støvmasse ad Gangen, og det er sandsynligt, at dette er det almindeligste Tilfælde, da de nederste Blomster, som længst have været udsprungne, sædvanligviis slet ingen Støvmasser indeholde, men de yngre, nys udsprungne, oftest have den ene tilbage. Saaledes fandt Darwin i Axet af en Orchis maculata ti Blomster, og det især de øvre, hvori der kun var een Støvmasse tilbage, men den hele Mekanisme var iøvrigt i Orden, saa at de kunde bortføres af Insekterne.

Hvad der hidtil er sagt om Indretningen hos Orchis mascula, passer i alt væsenligt ogsaa paa Orchis Morio, fusca, maculata og latifolia; derimod finder der en væsenlig Forskjel Sted hos Orchis (Anacamptis) pyramidalis (Horndrager — hos os meget sjelden i Skove paa Kalkgrund) *). Denne Art, der er afbildet i Fig. 3, har to

*) Med denne Art stemmer Orchis ustulata i det væsenlige overeens.

runde, heelt adskilte Ar (A, ss), et paa hver Side af den pungformede Snabel (r). Denne sidder ikke over Hon-

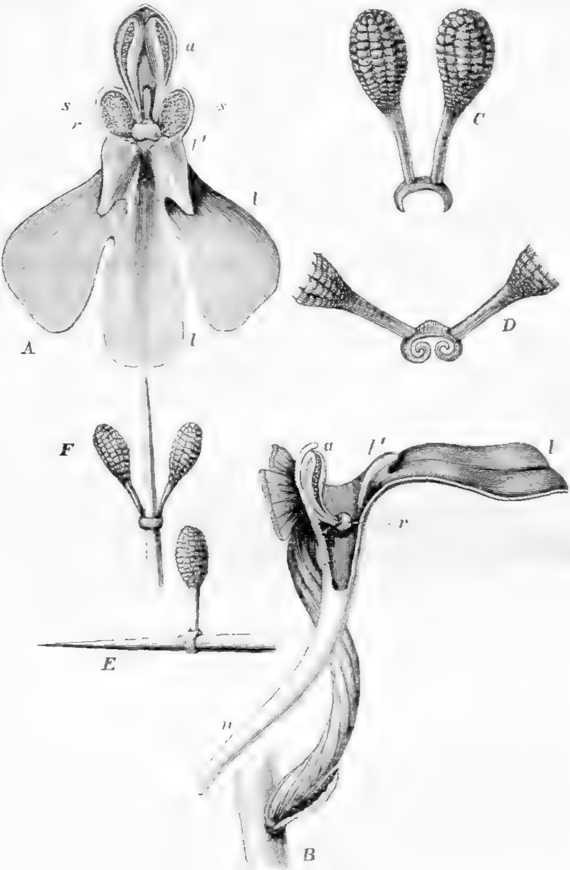

Fig. 3. Orchis pyramidalis.

A. Blomsten seet forfra. Alle Blade borttagne undtagen Læben. B Samme fra Siden. Den halve Læbe og et Stykke af det øverste af Læben bortskaarne. C. Begge Støvmasser paa den sadelformede Klæbeskive. D. Samme efter Sammentrækningen, naar den ikke er fasthæftet til noget. E. Støvmasserne, som have hæftet sig til en Naal, der er ført ind i Honninggjemmet. F. Samme efter at de have bøiet sig ned.

a Støvknappen. s. s Arret. r Snabelen. l Læben. l' Læbens Ribber. n Honningsporen.

ningsporen, men saa dybt, at den dækker og tildeels lukker dens Munding (smlg. B). Honninggjemmets Forkammer, der dannes af Læben og Griffelstøtten og er rummeligt hos Orchis mascula og dens beslægtede Arter, er her kun lille. Snabelen er forneden i Midten udhulet og fyldt med en Vædske. Der er kun een Klæbeskive af Form som en Sadel (C), der paa sin næsten flade Ryg bærer de to Støvmassers Stilke. Saalænge Snabelens Hud ikke er bristet, er det næppe muligt at see, at den sadelformede Skive udgjør en Deel af Snabelens sammenhængende Overflade, da den tildeels skjules og holdes fugtig af de to Støvknaprums Grundhinder, der foldes vidt ud over den. Skivens øvre Hud bestaaer af flere Lag smaa Celler og er derfor tyk; forneden er den overtrukket af et Lag meget fast klæbende Materie, som dannes i Snabelen.

Naar Snabelens Læbe er trykket ned ved en eller anden svag Berøring, blottes den nederste Deel af Klæbeskiven, som ikke forandrer sin Plads, og den kan nu klæbe sig fast til en Gjenstand, som berører den; et Haar er endogsaa stivt nok til trykke Læben ned, og Sadelens klæbrige Overflade hæfter sig da til det. Endelig er Læben forsynet med to ophøiede Ribber (A, l' og B, l'), der udenfra indad løbe skævt sammen imod Midten som en Fiskeruse og derved ere fortræffelig skikkede til at lede et bøieligt Redskab, som en Børste eller et Haar, ind i den lille, rundagtige og derhos tildels af Snabelen spærrede Munding af Honninggjemmet.

Naar nu en Sommerfugl — disse Dyr besøge meget hyppigt Orchideerne — stikker sin Sugesnabel ind mellem Læbens ledende Ribber, eller naar man efterligner denne Bevægelse med en fiin Børste, saa vil den ledes sikkert

ind i Honninggjemmets fine Munding og vil neppe kunne undgaae at trykke Snabelens Læbe ned. Derved kommer Børsten i Berøring med den sadelformede Skive, som nu er blottet og klæber sig fast og følger med tilligemed de to Støvmasser, naar Børsten trækkes tilbage: Saasnart Sadelen kommer ud i den frie Luft, pleier der øieblikkeligt at foregaae en rask Bevægelse med den, idet begge Endelapperne krumme sig indad og omfatte Børsten. Drages Støvmasserne derimod ud med en Tang, uden at Sadelen faaer noget at omfatte, saa rulle Enderne sig i Løbet af faa Sekunder tæt sammen (D). Mange Sommerfugles Snabel er saa tynd, at Sadelen netop omfatter den, saa at Enderne naae sammen under den, hvorfor en Naturforsker, der saae en Sommerfugl med Støvmasserne paa Snabelen, blev forledt til at troe, at den havde boret Snabelen midt igjennem Støvholderen.

Denne raske Sammenbøining tjener til at befæste Sadelen med dens Støvmasser oprette paa Sugesnabelen. Dog vilde dette kunne opnaaes alene derved, at Klæbestoffet størkner meget hurtigt, saa at den egenlige Hensigt snarere er, at Støvmasserne derved bøie sig ud fra hinanden. Thi da de sidde paa Sadelens flade Ryg, saa rage de i Begyndelsen lige op i parallel Retning, men alt som Sadelen krummer sig om Snabelen, maa de nødvendigviis bøies ud fra hinanden. Men neppe er denne Bevægelse endt, hvad der medtager en halv Snees Sekunder, før der begynder en anden Bevægelse, der ligesom den første alene bevirkes af den lille Hudskives Sammentrækning, og nu er ganske den samme, som før blev beskreven ved Orchis mascula, idet Støvmasserne fra den lodrette Stilling bøie sig i en ret Vinkel ned mod Snabelens Spidse, saa at de ligge parallelt med den (E. F).

Hensigten med denne dobbelte Bevægelse bliver klar, naar man fører Børsten med Støvmasserne tilbage, efterat Bevægelsen er endt (smlg. A og F). Thi nu have begge Støvmassernes Ender netop faaet en saadan Stilling, at den ene strøifer Arret paa den ene Side, den anden paa den anden Side, saa at de klæbrige Ar nu kunne løsne de elastiske Traade og fastholde nogle af Støvkornene.

Da der ikke hos andre Planter, neppe hos noget Dyr, findes fuldkomnere *Tilpasning af Organerne*, end hos disse Orchideer, saa fortjener det ovenfor beskrevne vel endnu engang at sammenfattes i Korthed. Blomsternes glimrende Farver tiltrække Dagsommerfuglene, deres eiendommelige Lugt Natsommerfuglene. Det øvre Bægerblad og de to øvre Kronblade danne en Hætte til Beskyttelse for Støvknappene og Arrene. Læben er udviklet til et langt Honninggjemme, hvis Indhold drager Sommerfuglene til og er saaledes opbevaret, — ganske anderledes end i andre Familier — at det kun langsomt kan opsuges for at give det klæbrige Stof under Sadelen Tid til at størkne. De sammenløbende Ribber paa Læben lede Sugesnabelen i den rigtige Retning, for at Støvmasserne ikke skulle komme til at sidde skjævt og gaae forbi Arrene. Snabelen er *opstillet paa Veien til Honningsaften som en Snare paa* Vildtets Vei; den er saaledes bygget, og de Linier, hvorefter den brister, saaledes dragne, at Sadelen dannes foroven, Pungens Læbe forneden. Denne Læbe er saa let at trykke ned, at Klæbeskiven ikke godt kan undgaae at blottes og hæfte fast ved Insektets Sugesnabel, og skulde det ikke skee, saa springer den elastiske Læbe igjen op, bedækker paany den klæbrige Flade og holder den fugtig til næste Gang. Vi see fremdeles, at det klæbrige Stof i

Snabelen er befæstet alene til Klæbeskiven og omgivet af Vædske, saa at det ikke kan størkne, før Skiven drages ud, ligesom Sadelens Overflade holdes fugtig indtil Uddragningen, da den eiendommelige Bøining af Støvmasserne begynder, først til Siden og saa fremad, en Bøining, der er nøiagtigt beregnet paa at bringe begge Støvmassernes Ender i Berøring med Arfladerne. Disse Flader ere klæbrige nok til at fastholde nogle Støvpakker, medens de overlade Resten til andre Blomster. — Endvidere maa mærkes, at selv om Insektet bruger lang Tid til at opsuge Honningsaften, saa begynder Støvmassernes Bøining ikke, før de ere trukne fuldstændigt ud af deres Rum, og at deres Bevægelse først et halvt Minut efter er saa vidt fuldendt, at de kunne træffe Arrene, naar de paany føres ind i en Blomst, saa at Insektet faaer Tid nok til at flyve til en ny Plante og saaledes befrugte den med en andens Støv.

De hidtil omtalte Orchis-Arter behøve nødvendigviis Insekters Medvirkning til deres Befrugtning. Dette fremgaaer af, at Støvmasserne ligge saa fast i deres Rum og Klæbeskiverne i Snabelen, at de ikke kunne rystes ud; men Darwin har yderligere godtgjort det ved Forsøg, idet han bedækkede adskillige Planter med Glasklokker, saa at Adgangen spærredes for Insekterne, hvorved det viste sig, at ingen Bestøvning fandt Sted og ingen Frø ansattes, skjøndt Planterne iøvrigt intet led.

Det synes efter Darwins Iagttagelser især at være Sommerfugle, der bestøve Orchis-Arterne; han nævner 23 Arter, paa hvis Snabel han har fundet Støvmasser af Orchis pyramidalis. Dog deeltage ogsaa mindre Insekter, f. Ex. Empis-Arter, i Bestøvningen og bortføre Støvmasserne paa Hovedet eller Brystet. Hvorvidt derimod Darwins

Mening, — at *nogle sjeldne Arter*, f. Ex. *Orchis fusca*, skulde vedblive at være saa sjeldne, fordi de ikke tiltrække Insekter nok, eller fordi de kun besøges af enkelte Arter, — er rigtig, turde være tvivlsomt, da Grunden ligesaa vel kan søges i andre Forhold, og Jordbunden aabenbart har megen Indflydelse herpaa.

Men endnu staaer der tilbage at omtale en mærkelig Omstændighed ved de omtalte Orchis-Arter, nemlig at deres »Honninggjemme«, som skulde lokke Insekterne til, ingen Honningsaft indeholder! Sprengel har undersøgt de fleste Arter, flere andre efter ham, og Darwin har anstillet mangfoldige Undersøgelser til de forskjelligste Tider, selv om Natten, i Solskin og i Regnveir, men selv ved Hjælp af Mikroskopet har han aldrig fundet mindste Spor af Saft i Honningsporen. Hvorledes skal man forklare sig dette? — Sprengel kaldte disse Blomster »Scheinsaftblumen«; han antog, at her fandt et systematisk Bedrageri Sted, at Insekterne, uagtet de bestandig skuffedes, dog bestandig kom igjen for at søge Honningsaft; men vi maa give Darwin Ret i, at det er umuligt at troe paa et saa kæmpemæssigt Bedrageri, naar man erindrer, hvor uhyre ofte det maatte gjentages. Og naar man husker, at Bestøvningen forudsætter, at Insektet gjentager sit Besøg hos disse Blomster flere Gange umiddelbart efter hinanden, saa maatte man, for at give Sprengel Ret, sætte Insekternes Forstand eller Instinkt meget lavt og kunde dog ikke forklare Grunden til, at disse Blomster vare saa overordenligt snildt indrettede, men at et af de vigtigste Led i Kjæden manglede. Imod Rigtigheden af Sprengels Mening taler ogsaa i høi Grad hvad Darwin har iagttaget, at monstrøse Blomster, som manglede Honninggjemmet, men hvis Befrugtningsapparat var i fuldstændig Orden,

ikke vare blevne berøvede deres Støvmasser, medens dette var Tilfældet med alle de fuldstændige Blomster i samme Ax. Et Forsøg, som Darwin anstillede ved at skjære Enden af Honninggjemmerne paa endeel Blomsterknopper hos Orchis pyramidalis, førte til et lignende Resultat, saa at Insekterne ikke synes at lade sig saa let narre.

Men hvor er da Nøglen til denne Gaade? Darwin synes at have fundet den, idet han bemærkede, at den indre og ydre Væg i Sporen hos disse Orchideer skilles ved et temmelig vidt Mellemrum, at dette er opfyldt af Vædske, og at den indre Væg eller Hinde er meget fiin og særdeles let gjennemtrænges af Vædsken; medens der ikke findes noget saadant Mellemrum hos Gymnadenia conopsea og Platanthera solstitialis *), hvis Sporer altid ere fyldte med fri Honningsaft. Han sluttede deraf, at Insekterne med deres Sugesnabel kunne gjennembore den fine Indrehud i hine Arters Honningsporer og opsuge Vædsken fra Mellemrummet. Naar man seer, hvor mange sindrige Foranstaltninger der ere trufne for Orchideernes Befrugtning, og af hvor stor Vigtighed det er, at Støvmasserne komme til at sidde fast paa Insektet og ikke falde til Siden eller tilbage, og naar man erindrer, at Klæbeskiven behøver nogen Tid for at sætte sig fast ved Saftens Størkning, saa at det vilde være til stor Nytte om Insektet blev lidt opholdt i at indsuge Saften, saa synes det ikke urimeligt at antage, at den usædvanlige Indretning, at Honningsaften afsondres indenfor Overhuden, er truffen her for at nøde Insekterne til et længere Ophold,

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*) Darwin nævner ikke, om det samme er Tilfældet med de andre Arter, hvis Sporer indeholde fri Honningsaft.

medens de paa flere Steder gjennembore denne Hinde og udsuge Saften af Mellemrummene.

Rigtigheden heraf bestyrkes ved en Undersøgelse af Klæbeskiven hos de Arter, hvis Sporer indeholde fri Honningsaft, nemlig Gymnadenia conopsea og albida, Platanthera *solstitialis og chlorantha og Coeloglossum viride.* Hos de fire første er Klæbeskiven ikke indesluttet i en Pung, men nøgen, hvoraf man strax seer, at den klæbrige Materie maa have en anden kemisk Beskaffenhed end Orchisarternes og ikke saa hurtigt størkne, hvilket Darwin ogsaa har overbeviist sig om ved Forsøg, der viste, at Skiven beholdt sin Evne til at klæbe sig fast i flere (2—24) Timer. Hos den sidste Art er Klæbeskiven vel bedækket af en pungformet Hinde, men denne er saa lille, at Botanikerne have overseet den, og Skiven bevarer ogsaa, ligesom de andre Arters, sin Klæbrighed i længere Tid efter Udtagelsen. Da den klæbrige Materie hos disse fem Arter altsaa formaaer at hæfte Støvmasserne tilstrækkelig fast paa Insekterne uden strax at størkne heelt*), saa vilde det ikke nytte, at Insekterne opholdtes længere med at suge Saften op, og derfor finde vi hos dem og hos dem alene Saften frit i Honninggjemmet. Hvis dette Sammenstød — paa den ene Side af et langsomt størknende Klæbestof og en Opbevaring af Honningsaften, der opholder Insekterne i længere Tid, paa den anden Side af et Klæbestof, der fra først af er meget seigt, og en Opbevaring af Saften, der tillader en hurtig Indsugning — er tilfældigt, saa er det et meget heldigt Tilfælde for disse

*) Det egenlig bevisende: at Klæbestoffet hos disse Arter strax er tilstrækkelig seigt til at lade Støvmasserne sidde saa fast som fornødent, har Darwin dog ikke paaviist. Den lange Tid der medgaaer til fuld Størkning synes derfor at tale for det modsatte.

Planter. Men er det ikke tilfældigt, saa er det et høist mærkeligt Exempel paa Tilpasning.

De øvrige indenlandske Arter af denne Gruppe (Slægterne: Gymnadenia, Platanthera, Coeloglossum, Herminium og Ophrys) skille sig fra de hidtil omtalte ved to adskilte Snabler. Neppe to Arter stemme iøvrigt overeens i Blomstens Indretning til Befrugtningen, men da Afvigelserne fra det i det foregaaende beskrevne ikke ere meget store, skal jeg indskrænke mig til at omtale et Par mærkeligere Tilfælde.

Hos Slægterne Ophrys og Herminium mangler Honningsporen, men erstattes af en Fordybning i Læbens nedre Deel, der dog, ligesom Orchisarternes Spore, ingen fri Honningsaft indeholder. At Klæbeskiven hos nogle Arter er nøgen og den klæbrige Materie derfor af en anden Beskaffenhed, er allerede omtalt. At Pungen, som indeslutter Klæbeskiven hos de fleste andre Arter, ikke er elastisk som hos Orchisarterne, hvor den igjen springer tilbage i sin Stilling, naar en Støvmasse er udtagen, — en Elasticitet, som her vilde være unyttig, da hver Snabel kun indeslutter 1 Klæbeskive, — er et Vidnesbyrd om Midlernes Tilpasning til det Maal, der skal naaes.

Hos Ophrys myodes og Coeloglossum viride (to Arter, der ere meget sjeldne her i Landet) findes der vel ogsaa en Pung, men den nederste Deel af Støvmassernes Stilk og Klæbeskivens øvre Deel ere ikke indesluttede deri, og da de saaledes ere udsatte for Luftens Paavirkning, mangle de den eiendommelige Evne til at bøie Støvmassen ned i Retning af Arret. Hos Ophrys myodes erstattes denne Mangel derved, at Stilken i sit naturlige Leie har en dobbelt Bøining næsten under en ret Vinkel; dog synes denne Indretning ikke tilstrækkelig til sit For-

maal, der kun kan opnaaes ved en gjentagen Hæven og Sænken af Insektets Hoved. Det staaer da efter al Sandsynlighed i Forbindelse hermed, at Støvmasserne hos denne Art efter Darwins Iagttagelser meget sjeldnere bortføres end hos de andre Orchideer, og at den kun meget sjeldent og sparsomt udvikler sine Frøkapsler. Indretningen hos Coeloglossum viride er meget afvigende og fortjener en nærmere Beskrivelse. Arret er her lille og stillet i Midten af Blomsten, medens Støvmasserne ligge høit over det, og de 2 Punge, der indeslutte Klæbeskivernes nedre Deel, ere fjernede langt fra hinanden ud til Siden af Blomsten, saa at et Insekt, der opsugede Honningsaften af Sporen, hvis Aabning findes lidt foran og under Arret, ikke vilde komme i Berøring med Klæbeskiverne, selv om det løftede Hovedet i Veiret. Men der er sørget for, at dette alligevel skeer, paa den mærkelige Maade, at der paa hver Side af Læbens Grund, lige under Klæbeskiverne, findes en lille Fordybning omgivet af Læbens ophøiede Rande, hvori der afsondres Honningdraaber. Tilmed er der en lang ophøiet Ribbe lige under det rigtige Honninggjemme, der leder Insekterne til at sætte sig paa Siden af Læben tæt ved det mindre Honninggjemme. Opsuge de nu først Saften af dette, ville de næppe kunne undgaae at bortføre Støvmassen, og naar de derefter vende sig til det egenlige Honninggjemme, vil den netop komme til at berøre Arret. Skjøndt det saaledes i Regelen vil være med Blomstens eget Støv, at Arret befrugtes, er en Krydsning mellem forskjellige Blomster dog ikke udelukket; i det Tilfælde nemlig at Insektet først opsugede Hovedbeholdningen og derefter Randdraaberne, vilde det flyve til den næste Blomst med

Støvmasserne paa Hovedet og kunde saaledes bestøve dennes Ar.

Før vi forlade denne Gruppe, maa vi endnu opholde os nogle Øieblikke ved **Ophrys apifera**, en i England og Sydeuropa, men ikke i Danmark, forekommende Art, fordi den, saavidt vides, er det eneste Exempel paa normal Selvbefrugtning af en Orchidee *). Dens to pungformede Snabler, Klæbeskiverne og Arrenes Stilling ere omtrent som hos de andre Ophrysarter, men Støvmassernes Stilke ere meget lange, tynde og bøielige, saa at de mangle den fornødne Stivhed til at holde sig oprette, som de ellers have hos alle Arter i Gruppen. Da Støvknappens to Rum ere bøiede stærkt fremad, have Stilkene foroven den samme Retning, og de pæreformede Støvmasser sidde derfor lige over Arrene. Strax efter Blomstens Aabning aabne ogsaa Støvknappens Rum sig, — og det usædvanlig vidt — og Støvmasserne falde ud. Da Stilkene ere saa svage, begynde de meget snart efter at synke nedad, saa at Støvmasserne hænge frit i Luften lige foran og i Høide med Arrene, medens Klæbeskiverne vedblive at holde deres nedre Ende fast i Pungen. En svag Luftstrømning er nu tilstrækkelig til at lade dem berøre Arret, ved hvilket de klæbe fast, hvad Darwin har overbeviist sig om ved Forsøg, idet han omgav Blomsterne med et Net, der holdt Insekter, men ikke Luftstrømme borte. Udelukkedes derimod Luftstrømningen, vedbleve Støvmasserne ogsaa at svæve i Luften foran Arret. Bestøvningen gaaer paa denne Maade saa regelmæssigt for sig i Naturen, at Støvmasserne næsten altid

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*) En meget mangelfuld Selvbefrugtning forekommer hos Cephalanthera grandiflora, som siden skal omtales.

findes paa deres Ar og Frøkapslerne næsten aldrig slaae feil — medens det omvendte er Tilfældet hos Ophrys myodes. — Det er unægtelig høist mærkeligt, at denne Indretning til Selvbefrugtning ikke findes hos de andre Ophrysarter, ikke engang hos Ophrys arachnites, der dog af flere Botanikere ansees for at være kun en Varietet af Ophrys apifera; og man fatter let, at Darwin af denne Omstændighed i Forbindelse med, at Ophrys apifera desuagtet har alle de nødvendige Indretninger til at befrugtes som de andre Arter, ledes til den Formodning, at der hos denne Art har skullet bevirkes en rigeligere Udvikling af Frø — hvad der kun kunde skee med Opgivelse af de Fordele, som Krydsningen kunde medføre; men at en saadan Krydsning med andre Individer dog i enkelte Tilfælde finder Sted, om end sjeldent. Dog, disse Gisninger kunne vi her lade staae hen.

Vi komme nu til en anden Hovedafdeling af Orchideerne, som have en fri, bag Arret stillet Støvknap. Støvkornene ere sammenlænkede ved fine, elastiske Traade, der tildeels hænge sammen og rage frem ved den øverste Ende af Støvmasserne og ere befæstede til Ryggen af Snabelen, hvorfor de mangle Stilken, der spiller en saa vigtig Rolle hos de forhen omtalte. Af de herhen hørende Slægter: Epipactis, Cephalanthera, Goodyera og Spiranthes skulle et Par Arter her nærmere omtales.

Hos Epipactis palustris (Sump-Huullæbe), der forekommer hist og her i vaade Enge, rager den forreste Deel af Arrene noget frem foran Griffelstøtten (Fig. 4, B, s og C, s). Paa dens Top sidder en enkelt lille, næsten kugleformet Snabel (B, r og C, r), hvis Forside rager noget frem foran Overfladen af Arrene, hvad der er af megen Vigtighed. I ung Tilstand bestaaer Snabelen af en skjør

Cellemasse med ru Yderflade; disse Yderceller forvandles under Udviklingen til en blød, glat og meget elastisk Hud, der er saa overordenlig fiin, at et Haar kan trænge igjen-

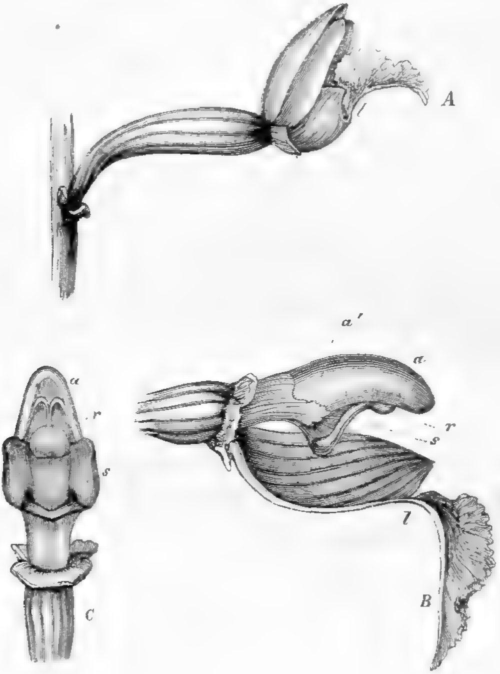


Fig. 4. Epipactis palustris.

A. Blomsten seet fra Siden; kun de nederste Bægerblade borttagne. B. Samme med alle Blade borttagne undtagen Halvdelen af Læben. C. Griffelstøtten seet forfra. Snabelen er i Afbildningen noget nedtrykt; den rager i Virkeligheden noget høiere op og skjuler mere af Støvknappens Rum.

a. Støvknappen, hvis to aabne Rum i C sees forfra a'. Rudimentær Støvknap. l. Læben. r. Snabelen. s. Arret.

nem den. Ved den svageste Gnidning, stundom maaskee ogsaa uden en saadan, bliver denne Overflade klæbrig, saa at Støvkornene blive hængende ved den. Denne bløde Yderhud danner en Kappe om Snabelen og er forinden overtrukken af et mere klæbrigt Lag, som i Luften størk-

ner i Løbet af 5—10 Minuter. Denne hele Kappe med dens indvendige Beklædning bortføres særdeles let, naar et Legeme skydes let imod den, i Retningen opad og tilbage, og der bliver da kun en lille Stump tilovers ved Grunden. I Knoppen rager Støvknappen ganske frit op bag Snabel og Ar; den aabner sig paalangs før Blomsten springer ud, saa at de to ovale Støvmasser ligge frit og løst i deres Rum. De bestaae af runde Smaakorn, der hænge sammen 4 og 4, og disse ere forbundne ved frie, elastiske Traade, der i Knipper strække sig langs Midterlinien af hver Støvmasses Forside, hvor de komme i Berøring med den øvre Deel af Snabelens Ryg, der før Blomstens Aabning er lænet mod Støvknappen, og fæste sig til dens Kappe. Derefter krummer Snabelen sig fremad og trækker derved Støvmassserne tildeels frem af deres Rum. Støvknappens øverste Ende bestaaer af en stump, solid Spids uden Støv, der rager noget frem over og foran Snabelen (B, a og C, a) Blomsterne staae næsten lodret ud fra Stængelen (A). Læben bestaaer af to Dele: den nederste danner en Skaal, der indeholder Honningsaft; den øverste, der kun hænger sammen med den nederste ved et smalt, bøieligt og meget elastisk Led, er krummet opad, saa at den tildeels lukker for Blomsten. En Flues Vægt er tilstrækkelig til at bøie den ned i den i B fremstillede Retning, men naar Vægten borttages, springer den igjen op i sin forrige Stilling.

Lad os nu see, hvortil alt dette tjener. At trykke Snabelen ned, som hos de forhen beskrevne Arter, løsner ikke Støvmasserne. Et Insekt, der satte sig paa Læbens øvre Deel for at suge Saften op, vilde slet ikke komme til at berøre Snabelen; naar det derimod var krøbet ind i Blomsten, og Læben altsaa havde lukket i for det ved at

rette sig op, vilde det være nødt til at kravle op ad Arret over Snabelen og den fremragende Ende af Støvknappen for igjen at komme ud. Eftergjør man nu denne Bevægelse med en Pensel, saa løsnes Snabelens Kappe med stor Lethed, klæber sig fast til Penslen og medfører Støvmasserne. Og hvor nøie alt er tilpasset til sin Bestemmelse, viser sig tydeligt her, idet Støvmasserne kun løsnes fuldstændigt, naar Penselen føres i Retning af den fremragende Ende af Støvknappen — den Vei, som Insektet maa tage for at slippe ud; føres den mere indad, saa følger der kun enkelte Støvklumper med. — Naar nu altsaa et Insekt paa sin Vandring ud af Blomsten har faaet Snabelens Kappe med de vedhængende Støvmasser befæstet til sit Hoved, og flyver til en anden Blomst, saa vil Arret være det første Sted, imod hvilket Støvmassen vil støde, og der vil den hæftes fast paa Grund af Arrets Klæbrighed. Og det er ikke uden Betydning, at den ydre Deel af Læben saa let bøies ned ved Insektets Vægt, da der saaledes aabnes saa stor en Indgang til Blomsten, at Støvmasserne ikke let komme i Berøring med Blomsterdækket, hvorved en Deel af Støvet vilde gaae til Spilde, da Støvmasserne meget let sønderrives.

Epipactis latifolia (bredbladet Huullæbe), som er almindelig i vore Skove, stemmer i det væsenlige overeens med den forrige Art; kun er Adgangen til Blomsten friere, idet Læbens ydre Led mangler Elasticitet og Støvknappens Ende ikke rager frem foran Snabelen, hvorfor Støvmasserne kunne bortføres uden at denne berøres. Derimod afviger Cephalanthera grandiflora (hvidguul Skovlilie) — som findes i Skove paa Kalkbund og tilhører en Slægt, der ellers staaer meget nær ved Epipactis — væsenligt fra denne og alle andre, idet Snabelen ganske

mangler. Støvkornene ere skilte — ikke forenede i Smaaklumper — og kun forbundne ved faa og svage elastiske Traade. Støvknappene aabne sig før Blomstens Udspringning og skyde Støvmasserne noget frem, saa at de staae næsten frit som to oprette Søiler, der fortil læne sig imod Arrets øvre Rand, der naaer op til omtrent $\frac{1}{3}$ af deres Høide (Fig. 5). De Støvkorn, som saaledes berøre Arrets skarpe Rand — men hverken de høiere eller lavere staaende — sende allerede før Blomsten er fuldkommen udsprungen en Mængde Støvrør dybt ind i Arrets Væv. Derefter krummer Arret sig fremad, saa at Støvsøilerne blive heelt frie fra Støvknappen og kun holdes oprette af Arret, hvortil de læne sig og hvormed de ere forbundne ved Støvrørenes Indtrængen i Arret. Uden denne Understøttelse vilde de snart falde om, uagtet Blomstens Stilling er opret og uagtet de ere beskyttede mod Vinden af Kronbladene og Læbens nedre Deel, der slutte sig tæt sammen om Griffelstøtten.

Fig. 5. Cephalanthera grandiflora.

Griffelstøtten seet fra Siden, efter at alle Bæger- og Kronblade ere borttagne. Støvsøilerne sees mellem Støvknap og Ar.

a. Støvkappen. p. Støvmasserne. s. Arret.

Læben bestaaer, som hos Epipactis, af to Dele, og naar Blomsten er fuldt udviklet, vender den øvre, trekantede Deel nedad i en ret Vinkel til den nedre Deel, saa at den danner en god Landingsplads for et Insekt foran en trekantet Aabning til den næsten rørformede Blomst. Kort efter at Blomsten er befrugtet, retter denne øvre Deel af Læben sig igjen op, tilslutter Aabningen og indeslutter fuldstændigt Befrugtningsorganerne. Darwin har

ikke fundet Honningsaft i Læbens nedre skaalformede Deel, men antager dog, at der afsondres en saadan.

Cephalanthera grandiflora *) synes altsaa at yde os det andet Exempel paa stadig Selvbefrugtning hos Orchideerne, eftersom endeel Støvkorn altid befrugte Arret, og Insekters Medhjælp kunde synes overflødig, da man kunde tænke sig, at Støvsøilerne ved at falde sammen, vilde sprede de andre Støvkorn over Arrets Flade. Darwin har imidlertid godtgjort ved Forsøg, at Støvsøilerne kun undtagelsesviis falde sammen, at Støvet altsaa ikke kommer til Arret, og at de fleste Frø blive golde, naar Blomsterne udelukkes fra Insekternes Besøg, medens Blomsternes Ar i fri Tilstand ere bedækkede med Støvkorn og Søilerne ganske nedbrudte. Det vilde ogsaa være forunderligt, om det skulde være uden Hensigt, at Læben en kort Tid aabner Indgang til Blomsten og siden lukkes, at Blomstens Form netop er saaledes, at et Insekt maatte krybe hen over Arret, og at Støvsøilerne ere stillede saaledes, at kun nogle faa Støvkorn komme til at virke, medens store Masser over og under disse bleve ubrugte.

Her synes altsaa at være et sammensat Tilfælde. Her finder en stadig, men meget ufuldstændig Selvbefrugtning Sted, der deels tjener til at erstatte Insekternes Hjælp, hvis den skulde udeblive, deels til at lette Insekternes Arbeide ved at holde Støvsøilerne oprette. Men denne ufuldstændige Befrugtning suppleres ved Besøg af Insekter, der sprede Støvet over Arret af samme Blomst, men tillige maa føre en Deel med sig til andre Blomster, saa at her kun tildeels finder en Undtagelse Sted fra den al-

*) De to andre Arter af denne Slægt, som forekomme her i Landet, omtaler Darwin ikke.

mindelige Regel, at den ene Blomst befrugtes af de andre Blomsters Støv.

Derimod afgiver Spiranthes autumnalis (Høst-Skrueax) — en her i Landet meget sjelden Art — Exempel paa en Orchidee, der ikke alene nødvendig behøver Insekters Medhjælp ved Bestøvningen, men hvor desuden den ene Blomst kun kan bestøves med den andens Sædstøv, hvad en kort Beskrivelse af Blomstens Bygning vil godtgjøre. Blomsterdækket danner et Rør omkring Griffelstøtten, og paa den Tid, da Blomsten aabnes, er Læbens ydre Deel vel saaledes nedadbøiet, at Insekter kunne sætte sig derpaa, men dens indre Deel slutter saa tæt op til Snabelen — her en lang, tynd og flad Fremragning — og det derunder skraat fremragende Ar (Fig. 6 r, s), at kun en fiin Rende, foroven dannet af Snabelens lidt udhulede Forside, forneden af en Huulhed i Læben, fører ind forbi Arret til Læbens Ende, hvor Honningsaften opbevares (n). Da Snabelen rager langt frem over Arret og under Støvknappen — Blomstens Stilling er nemlig vandret — og altsaa danner en Skillevæg mellem Arret og Støvet, kan dette ikke befrugte hiint uden saaledes, at Støvmasserne først bortføres fra deres Plads og derpaa føres ind til Arret; men paa den Tid er Indgangsaabningen til Arret altfor snever til at Støvmasserne kunne bringes derind. Insekterne, som besøge Blomsterne strax

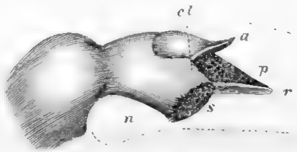


Fig. 6. Spiranthes autumnalis.

En moden Blomst efter at Læben (hvis Omrids er punkteret) har fjernet sig fra Snabelen. Alle Blade ere bortskaarne, men de øvre Bægerblades Stilling ligeledes antydet ved Punkter.
a. Støvknappen. n. Honninggjemmet. p. Støvkornene. r. Snabelen. s. Arret.

efter deres Aabning, kunne derfor vel opsuge Honningsaften, og idet de trække deres Sugesnabel tilbage, ville Støvmasserne følge med ud af Blomsten, men de formaae ikke at bringe dem i Berøring med Arret. Det er først et Par Dage senere, at Læben fjerner sig saameget fra Snabelen, at Aabningen bliver stor nok til at tilstede Støvmasserne, som sidde paa Insektets Sugesnabel, Adgang til Arret. Hvorledes skeer da Bestøvningen? Det skal strax blive paaviist, men først maa det i Korthed forklares, hvorledes Støvmasserne, der sidde i Støvknappen over Snabelen, kunne bortføres med Insektets Sugesnabel, der stikkes ind under Snabelen. Denne bestaaer nemlig af en Slags togrenet Gaffel, og Mellemrummet mellem Grenene udfyldes paa Bagsiden (den øverste Side) af en langstrakt Skive, der er fyldt med klæbrig Vædske, som i Luften størkner i Løbet af 1 Minut, men allerede efter 4—5 Sekunders Forløb klæber en Gjenstand fast. Paa Forsiden er der en Huulning mellem Grenene og i denne er Huden saa skrøbelig, at den brister ved den svageste Berøring og det ikke blot i Huulningen, men langs Klæbeskivens Rande, saa at denne selv bliver fri og udsveder saamegen Vædske, at den fastgjøres ved det Legeme, der har foraarsaget Riften og bortføres med det. Men med denne Klæbeskive følger da med det samme Støvmasserne, hvis Traade have befæstet sig dertil allerede før Blomstens Aabning, da Støvknappens Rum nemlig aabne sig før Blomsten og Støvmasserne ligge tæt op til Snabelens Ryg. Det er altsaa indlysende, at en Humlebi — det skal især være disse, der besøge Spiranthes, — ikke kan føre sin Snabel ind i den fine Rende, hvis Overside netop er Snabelens Huulning, uden at Støvmasserne ville hæfte sig fast og bort-

føres. Men nu er disse Dyrs Fremgangsmaade den, at de først sætte sig paa den nederste Blomst i Axet, der er snoet i Spiral, og derpaa krybe opad fra Blomst til Blomst, idet de følge Spirallinien. De komme altsaa først til de ældste, længst udsprungne Blomster, sidst til de sidst udsprungne. Gik de den modsatte Vei, vilde Støvet spildes. Nu finde de Støvet allerede bortført i de ældre Blomster; naar de komme til de nys udsprungne, endnu ikke besøgte Blomster, uddrage da Støvmasserne og flyve saa til en ny Plante, hvor de begynde paa samme Viis, og hvor nu Bestøvningen kan gaae for sig i de ældre Blomster, idet, som ovenfor viist, Læben nu har fjernet sig tilstrækkeligt fra Arret. I de øvre Blomster hentes nyt Støv og saaledes fremdeles. Darwin har fanget Humlebier med indtil 5 Hæfteskiver paa Snabelen. Idet de saaledes hente Honning til sig selv, sørge de tillige for at Spiranthes forplanter sig og kan berede Honning til nye Generationer af Humlebier.

I den tredie og sidste Afdeling af de indenlandske Orchideer, af hvilken Darwin omtaler Slægterne: Malaxis, Listera og Neottia, er ingen Deel af Snabelens Overhud vedvarende befæstet til Støvmasserne. Hos Malaxis paludosa (Sump-Hjertelæbe) — den mindste af de danske Orchideer — foregaaer Befrugtningen meget let og simpelt, idet Støvmasserne ved Blomstens Aabning ligge frit — Støvknappen skrumper nemlig meget tidligt sammen — og kun med deres øvre spidse Ende støtte sig til Snabelens Top, hvor de fastholdes af en lille Draabe klæbrig Vædske; denne Draabe vil et Insekt, der stikker Hoved eller Snabel ind i Blomsten, nødvendig maatte berøre og vil saaledes medføre Støvmasserne til andre Blomster,

hvor de ville træffe Arret ifølge deres Stilling paa Insæktets Hoved eller Snabel.

Derimod foregaaer Befrugtningen hos de to andre Slægter paa en meget mærkelig Maade. Det vil være tilstrækkeligt at omtale Listera ovata (ægbladet Fliglæbe) — der er temmelig almindelig i fugtige Skove — da de andre sjeldnere Arter i alt væsenligt stemme overeens med denne.

Snabelen (Fig. 7, r), som hvælver sig ud over Arfladen (s), er bladagtig, stor og tynd, foran hvælvet, bagtil fordybet og paa begge Sider af den spidse Top noget udhulet. Støvknappen aabner sig allerede i Knoppen, saa at Støvmasserne ligge fuldkommen frie i de udsprungne Blomster, lænede til Snabelens Ryg. Denne bøier sig nu lidt frem- og nedad imod Arfladen, hvorved den fjernes noget fra Støvknappens Spids (a). Naar man nu berører Snabelens Spids — om ogsaa blot med et fint

Fig. 7. Listera ovata.

Blomsten seet fra Siden; alle Blade borttagne undtagen Læben.

a. Støvknappen. col. Griffelstøttens Top. l. Læben. n. Læbens Honningfure p. Støvmassen. r. Snabelen. s. Arret.

Haar — saa springer der øieblikkelig en Draabe klæbrig Vædske frem af den, der træffer den spidse Ende af Støvmasserne (p), som hvile paa Snabelens Ryg. I Løbet af 2—3 Sekunder størkner denne Draabe og bliver meget haard. Havde Snabelen ikke i Forveien bøiet sig lidt frem, vilde den træffe Spidsen af Støvknappen og saaledes lukke til for Støvet; nu træffer den kun Støvmassernes Spids og Hovedet af det Insekt, der har bevirket Explosionen, og fasthæfter saaledes Støvet til dette.

Blomsterne besøges af en stor Mængde Insekter, der opsuge Honningsaften, som afsondres i en lang, smal Fure midt i Læben (n), og denne Fure fortsættes opad den lange Læbe indtil dens Grund under Arret. Naar Insektet er kommet hertil og løfter Hovedet op for at flyve bort, vil det træffe Snabelens Spids og frembringe den ovenfor beskrevne Virkning. Darwin har fanget flere Individer af Slægterne Hemiteles og Cryptus, der kom ud af Blomsten med Støvmasserne befæstede til den indre Øierand. Ganske smaa Insekter, som ikke have Kraft til at bortføre Støvmasserne, blive undertiden hængende og omkomme.

I det Øieblik, da Snabelen saaledes har udsendt sin Draabe, krummer den sig endnu mere frem og nedad, saa at den danner en ret Vinkel med Arret; derved beskytter den dette, men forhindrer tillige Befrugtningen, saa at det her ligesom hos Spiranthes er de yngre Blomsters Støv, der befrugte de ældre Blomsters Ar; thi i Løbet af nogle Timer eller en Dag, i hvilken Tid Arret udvikler meget mere Klæbrighed, bøier Snabelen sig atter tilbage, indtil den faaer en ganske opret Stilling, og Adgangen til Arret bliver fri, saa at Støvmasserne kunne berøre det, dets Klæbrighed fastholde Støvkornene, sønderrive Traa-

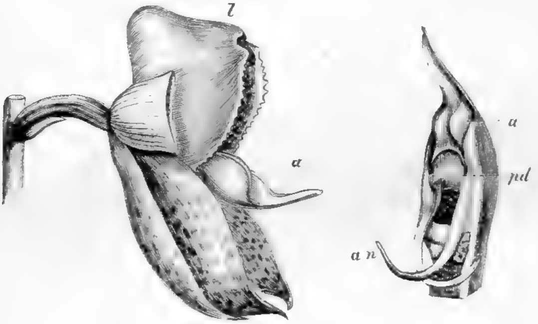
dene, hvormed de ere forbundne, og Befrugtningen saaledes gaae for sig.

Darwins Undersøgelser omfatte endnu foruden disse Slægter en stor Mængde tropiske Orchideer, der frembyde mangfoldige Afvexlinger i de Tilpasninger, hvorved Insekterne kunne udføre Bestøvningen. Da hans Materiale til Undersøgelsen af disse imidlertid har været mindre rigt end til de indenlandske, og derfor de fleste endnu trænge til nærmere Undersøgelse, og da næsten alle dette Tidsskrifts Læsere ville savne Materiale til at eftersee de beskrevne Forhold i Naturen, hvad Afbildninger kun ufuldstændigt kunne erstatte, maa jeg henvise dem, der kunde ønske en fuldstændigere Kundskab, til Darwins eget Værk. Jeg skal kun undtagelsesviis omtale en enkelt Slægt, hvor Befrugtningen foregaaer ved en endnu mærkeligere Explosion, end den sidst beskrevne, Slægten Catasetum, der desuden frembyder den Særegenhed, at Kjønnene ere adskilte, saa at det kun er undtagelsesviis, at der paa samme Plante forekommer baade Han- og Hun-Blomster; og disses Bygning er saa forskjellig, at de have været henførte til ganske forskjellige Slægter *).

Hos Catasetum (hvoraf Darwin har undersøgt 3 Arter) mangler Arret Klæbrighed til at fastholde Støvkornene, Æggene ere uudviklede og skulle heller ikke i deres Hjemstavn nogensinde udvikle sig til Frø; Frøkapslen er ogsaa meget kort og tynd. Derimod er det hos Monachanthus Støvmasserne, der ere aldeles rudimentære, deres

*) Catasetum tridentatum (Hanblomst. Fig. 8), Monacanthus viridis (Hunblomst, Fig 9 A) og Myanthus barbatus (Tvekjønsblomst, Fig 9 B) fandtes af R. Schomburgk og senere af Flere paa en og samme Plante. Til andre Catasetum-Arter kjender man endnu ikke Hunplanterne.

Rum aabne sig ikke, og de mangle Snabelens vigtigste Organer, medens Ar og Æg ere fuldkomment udviklede. Hos Myanthus endelig findes Bestøvningsredskaberne, Ar og Æg omtrent ligeligt udviklede. Kun hos denne sidste kunde altsaa en Befrugtning ved eget Støv foregaae. For at overføre Støvet fra Catasetum (tridentatum) til Monacanthus behøves nødvendigt Insekters Medhjælp, og dertil er der truffet en høist mærkelig Række af Foranstaltninger.



A B

Fig. 8. Catasetum tridentatum.

A. Blomsten fra Siden; 2 Bægerblade bortskaarne. B. Griffelstøtten opret og seet forfra.
a. Støvknappen. an. Snabelens Følehorn. l. Læben. pd. Klæbeskivens Fod. (Klæbeskiven selv er skjult i det mørke Rum — Argruben — under denne).

Støvmasserne ere ved en temmelig solid og meget elastisk Fod forbundne med en stor Klæbeskive. Men denne er utilgængelig for Insekter, da den ligger gjemt i en Grube (der hvor Arret skulde være) med sin klæbrige Deel trykket op mod Loftet, saa at Insekter, selv om de trængte derind, hvortil der ingen Anledning er, ikke vilde komme i Berøring dermed. Men Klæbeskivens elastiske Fod (Fig. 8 pd) er bøiet over Snabelen og holdes i denne Stilling som en spændt Bue ved en fiin Hinde, der er sammenvoxet med to lange, hule Følehorn (an), der ud-

gjøre en Deel af Snabelen og bøie sig ned foran Argruben og ere gjemte i Læbens Huulhed. Disse Følehorn ere i den Grad følsomme, at Berøring med en Børste i deres Spidse eller et andet Sted paa dem øieblikkeligt foraar-

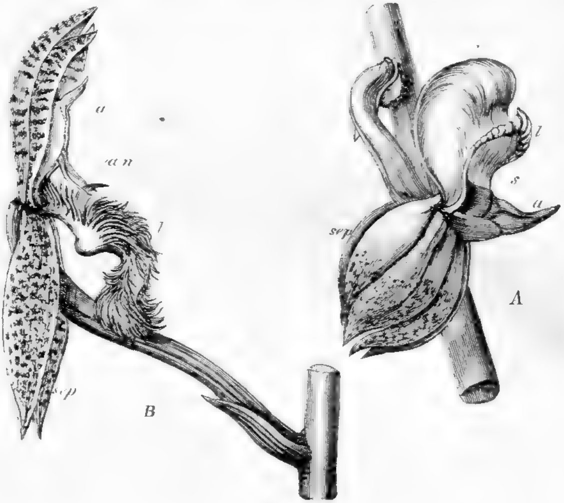


Fig. 9.

A. Monacanthus viridis seet fra Siden. B. Myanthus barbatus ligeledes.
a. Støvknappen. an. Følehornene. l Læben. s. Arret. sep. Bægerblade.

sager en Bristen af den omtalte Hinde ved deres Grund (uden at der iøvrigt foregaaer nogen kjendelig Indvirkning paa Følehornene selv). Derved bliver Klæbeskivens Fod fri, og i samme Nu retter den bøiede Fod sig ud med en saadan Kraft, at den slynger Klæbeskiven frem og flyver 2—3 Fod ud i Luften medførende Støvmasserne. Klæbeskiven slynges altid foran og vil efter al Sandsynlighed træffe det Insekt i Hovedet, som ved at gnave paa Læben og saaledes at berøre Følehornene har bevirket Explosionen. Her hæfter den sig fast, og Støvmassen føres saaledes med, indtil den paa Monachanthus, — hvor hele

dette Apparat mangler, men hvor der i Stedet er et klæbrigt Ar — finder en Plads beredt for Støvet. Følehornene ere det eneste Sted i Blomsten, hvis Berøring befrier Støvmasserne, men de udføre det ogsaa med Sikkerhed. I Sandhed, en mærkelig Foranstaltning! Støvmasserne udsendes som Pile, der maa træffe Insekterne for saaledes at bortføres til det Sted, hvor de skulle virke. En sindrigere Tilpasning findes vel neppe nogensteds i Naturen.

Det er vist intet forgjæves Haab, Darwin udtaler, at Meddelelsen af disse Kjendsgjerninger fra Orchideernes eiendommeligt og mangfoldigt uddannede Familie vil foranledige, at mange iagttage de indenlandske Arters Liv nøiere. En Undersøgelse af deres sindrige Indretninger kan ikke andet end give mange et høiere Begreb om hele Planteriget og vil være tiltalende saavel for den, der anseer alt i det for afhængigt af Naturlove, som for den, der i alt seer Skaberens umiddelbare Indgriben.

De menneskelignende Aber: Orang'ens, Chimpansens og Gibbonernes Levemaade og Naturhistorie.

Efter Huxleys »Evidence as to man's place in nature«. London 1864.

Spørgsmaalet om Menneskets Forhold til Dyreriget og navnlig til Aberne, i systematisk Henseende, har oftere været paa Bane og er navnlig bleven meget drøftet i de senere Aar, da Spørgsmaalet om Arternes Oprindelse og det hele organiske Livs Udviklingshistorie paa Jorden har sat ikke alene den videnskabelige Verden, men ogsaa den uvidenskabelige (men just ikke ulidenskabelige) Almeenhed i en vis Bevægelse. Anskuelserne have staaet saa langt fra hverandre, som vel var muligt; medens nogle oprettede et eget Rige for Mennesket*), ansaae andre Slægtskabet mellem Mennesket og Aberne for at være saa inderligt, at de ikke toge i Betænkning at erklære, at Mennesket maatte nedstamme (gjennem den hypothetiske Darwinske Artsmetamorphose) fra en eller anden Abeform. Diskussionen herom har havt den gode Følge, at der derved er kastet en heel Deel Lys over Forholdet mellem Mennesket og Aberne i zoologisk Henseende; om de Kjendsgjerninger, som i denne Henseende komme i Betragtning, kan der i al Fald neppe disputeres

*) See dette Tidsskrift 2 Række. 3 Bd

Cœlanthium, limited to two Cape species, differs from *Pharnaceum* as *Thylacospermum* from *Arenaria*, by the union of the sepals at the base into a campanulate tube, round the edge of which are inserted the stamens, being thus much more decidedly perigynous than in the rest of the group.

The genera *Psammotrophe*, Eckl. & Zeyh., and *Polpoda*, Presl, with uniovulate cells to the ovary, enumerated by Fenzl among Mollugineæ, appear to have nothing to distinguish them from true Phytolaccaceæ. *Adenogramma*, Presl, is also a Phytolaccaceous plant allied to *Giesekia*, where the ovary and fruit are reduced to a single one-seeded carpel, not compounded of 2 or 3 carpels although one-seeded as in Paronychiaceæ. *Acrossanthes*, on the other hand, both in habit and character, belongs to the apetalous Ficoideæ.

IV. Paronychiaceæ.

Without having sufficiently examined all the genera of this Order to ascertain their limits with respect to each other, or the order of their arrangement, we have, however, verified the ordinal characters in all the following (except *Cardionema*):—

1. *Corrigiola*, Linn. (an exceptional genus in its prominent petals and alternate leaves); 2. *Herniaria*, Linn.; 3. *Illecebrum*, Linn.; 4. *Cardionema*, DC.; 5. *Pentacæna*, Bartl.; 6. *Paronychia*, Juss. (including *Siphonychia*, Torr. et Gray, and *Anychia*, Rich., and perhaps altogether, with *Cardionema* and *Pentacæna*, artificial sections of *Illecebrum*); 7. *Habrosia*, Fenzl; 8. *Sclerocephalus*, Boiss.; 9. *Gymnocarpos*, Forsk.; 10. *Pteranthus*, Forsk.; 11. *Cometes*, Burm.; 12. *Dicheranthus*, Webb; 13. *Pollichia*, Soland.; 14. *Guilleminea*, H. B. et K.; 15. *Mniarum*, Forst.; 16. *Scleranthus*, Linn.; and 17. *Lastarriea*, A. Gay.

On the Two Forms, or Dimorphic Condition, in the Species of *Primula*, and on their remarkable Sexual Relations. By Charles Darwin, M.A., F.R.S., F.L.S., &c.

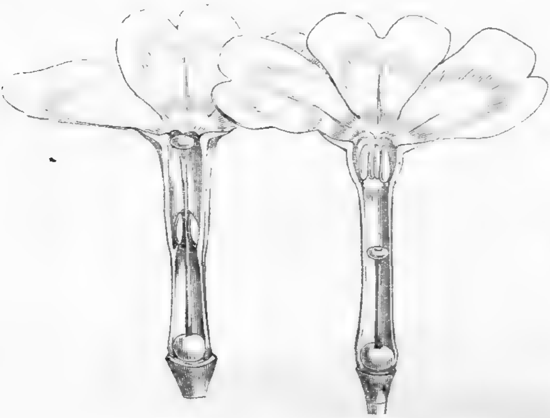
[Read Nov. 21, 1861.]

If a large number of Primroses or Cowslips (*P. vulgaris* and *veris*) be gathered, they will be found to consist, in about equal numbers, of two forms, obviously differing in the length of their pistils and stamens. Florists who cultivate the Polyanthus and Auricula are well aware of this difference, and call those which display the globular stigma at the mouth of the corolla "pin-headed" or "pin-eyed," and those which display the stamens "thumb-eyed." I

Mo. Bot. Garden,
1896.

will designate the two forms as long-styled and short-styled. Those botanists with whom I have spoken on the subject have looked at the case as one of mere variability, which is far from the truth.

In the Cowslip, in the long-styled form, the stigma projects just above the tube of the corolla, and is externally visible; it stands high above the anthers, which are situated halfway down the tube,



Long-styled. Short-styled.

and cannot be easily seen. In the short-styled form the anthers are attached at the mouth of the tube, and therefore stand high above the stigma; for the pistil is short, not rising above halfway up the tubular corolla. The corolla itself is of a different shape in the two forms, the throat or expanded portion above the attachment of the anthers being much longer in the long-styled than in the short-styled form. Village children notice this difference, as they can best make necklaces by threading and slipping the corollas of the long-styled flowers into each other. But there are much more important differences. The stigma in the long-styled plants is globular, in the short-styled it is depressed on the summit, so that the longitudinal axis of the former is sometimes nearly double that of the latter. The shape, however, is in some degree variable; but one difference is persistent, namely, that the stigma of the long-styled is much rougher: in some specimens carefully compared, the papillæ which render the stigmas rough were in the long-styled form from twice to thrice as long as in the short-styled. There is another and more remarkable difference, namely, in the size of the pollen-grains. I measured with the micrometer many

specimens, dry and wet, taken from plants growing in different situations, and always found a palpable difference. The measurement is best made with grains distended with water, in which case, the usual size of the grains from short-styled flowers is seen to be $\frac{10-11}{7000}$ of an inch in diameter, and those from the long-styled about $\frac{7}{7000}$ of an inch, which is in the proportion of three to two; so that the pollen-grains from the short stamens are plainly smaller than those from the long stamens which accompany the short pistil. When examined dry, the smaller grains from the long-styled plants are seen under a low power to be more transparent than the larger grains, and apparently in a greater degree than can be accounted for by their less diameter. There is also a difference in shape, the grains from the short-styled plants being nearly spherical, those from the long-styled being oblong with the angles rounded; this difference in shape disappears when the grains are distended with water. Lastly, as we shall presently see, the short-styled plants produce more seed than the long-styled.

To sum up the differences:—The long-styled plants have a much longer pistil, with a globular and much rougher stigma, standing high above the anthers. The stamens are short; the grains of pollen smaller and oblong in shape. The upper half of the tube of the corolla is more expanded. The number of seeds produced is smaller.

The short-styled plants have a short pistil, half the length of the tube of the corolla, with a smooth depressed stigma standing beneath the anthers. The stamens are long; the grains of pollen are spherical and larger. The tube of the corolla is of the same diameter till close to its upper end. The number of seeds produced is larger.

I have examined a large number of flowers; and though the shape of the stigma and the length of the pistil vary, especially in the short-styled form, I have never seen any transitional grades between the two forms. There is never the slightest doubt under which form to class a plant. I have never seen the two forms on the same plant. I marked many Cowslips and Primroses, and found, the following year, that all retained the same character, as did some in my garden which flowered out of their proper season in the autumn. Mr. W. Wooler, of Darlington, however, informs us that he has seen the early blossoms on Polyanthuses which were not long-styled, but which later in the season produced flowers of this form. Possibly the pistils may not in these cases have become fully developed during the early spring. An excellent

proof of the permanence of the two forms is seen in nursery gardens, where choice varieties of the Polyanthus are propagated by division; and I found whole beds of several varieties, each consisting exclusively of the one or the other form. The two forms exist in the wild state in about equal numbers: I collected from several different stations, taking every plant which grew on each spot, 522 umbels; 241 were long-styled, and 281 short-styled. No difference in tint or size could be perceived in the two great masses of flowers.

I examined many cultivated Cowslips (*P. veris*) or Polyanthuses, and Oxlips; and the two forms always presented the same differences, including the same relative difference in the size of the pollen-grains.

Primula Auricula presents the two forms; but amongst the improved fancy kinds the long-styled are rare, as these are less valued by florists, and seldomer distributed. There is a much greater relative inequality in the length of the pistils and stamens than in the Cowslip, the pistil in the long-styled form being nearly four times as long as in the short-styled, in which it is barely longer than the ovarium; the stigma is nearly of the same shape in both forms, but it is rougher in the long-styled, though the difference is not so great as in the two forms of the Cowslip. In the long-styled plants the stamens are very short, rising but little above the ovarium. The pollen-grains of these short stamens from the long-styled plants, when distended with water, were barely $\frac{5}{6000}$ of an inch in diameter, whereas those from the long stamens of the short-styled plants were barely $\frac{7}{6000}$, showing a relative difference of five to seven. The smaller grains of the long-styled plants were much more transparent, and before distention with water more triangular in outline than those of the other form. In one anomalous specimen with a long pistil, the stamens almost surrounded the stigma, so that they occupied the position proper to the stamens of the short-styled form; but the small size of the pollen-grains showed that these stamens had been abnormally developed in length, and that the anthers ought to have stood at the base of the corolla.

In the two forms of *Primula Sinensis*, the pistil is about twice as long in the one as in the other. The stigma of the long-styled varies much in shape, but is considerably more elongated and rougher than that of the short-styled, the latter being nearly smooth and spherical, but depressed on the summit. The shape of the throat of the corolla in the two forms differs as in the Cow-

slip, as does the length of the stamens. But it is remarkable that the pollen-grains of both forms, wet and dry, presented no difference in diameter; they vary somewhat in size, as do the pollen-grains of all the species, but in both forms the average diameter was rather above $\frac{10}{6000}$ of an inch. There is one remarkable difference in the two forms of this species, namely (as we shall presently more fully see), that the short-styled plants, if insects be excluded and there be no artificial fertilization, are quite sterile, whereas the long-styled produce a moderate quantity of seed. But when both forms are properly fertilized, the short-styled flowers (as with Cowslips) yield more seed than the long-styled. In a lot of seedlings which I raised, there were thirteen long-styled and seven short-styled plants.

Of *Primula ciliata* a long-styled specimen, and of *P. ciliata*, var. *purpurata*, a short-styled specimen, were sent me from Kew by Prof. Oliver. This case, however, is hardly worth giving, as the variety *purpurata* is said* to be a hybrid between this species and *P. auricula*; and the height of the stamens in the one form does not correspond with the height of the stigma in the other, as they would have done had they been the same species. There was, however, the usual difference in the roughness of the stigmas in the two forms, and the pollen-grains, distended in water, measured $\frac{6}{6000}$ and $\frac{4-5}{6000}$ of an inch in diameter. Single trusses were sent me of *P. denticulata* and *P. Piedmontana* which were long-styled, and of *P. marginata* and *nivalis* which were short-styled; and the general character of the organs leaves hardly any doubt on my mind that these species are dimorphic. In a single flower of *P. Sibirica*, however, which was sent me from Kew, the stigma reached up to the base of the anthers; so that this species is not dimorphic, or not dimorphic as far as the length of the pistil and stamens are concerned, unless indeed this single specimen was anomalous, like that mentioned of *P. auricula*.

We thus see that the existence of two forms is very general, if not universal, in the genus *Primula*. The simple fact of the pollen-grains differing in size and outline, and the stigma, in shape and roughness, in two sets of individuals of the same species, is curious. But what, it may be asked, is the meaning of these several differences? The question seems worthy of careful investigation, for, as far as I know, the use or meaning of dimorphism in plants has never been explained; hence, I will give my obser-

* Sweet's 'Flower Garden,' vol. v. tab. 123.

vations in detail, though I am far from supposing that all cases of dimorphism are alike. The first idea which naturally occurred was, that the species were tending towards a dioicous condition; that the long-styled plants, with their rougher stigmas, were more feminine in nature, and would produce more seed; that the short-styled plants, with their long stamens and larger pollen-grains, were more masculine in nature. Accordingly, in 1860, I marked some Cowslips of both forms growing in my garden, and others growing in an open field, and others in a shady wood, and gathered and weighed the seed. In each of these little lots the short-styled plants yielded, contrary to my expectation, most seed. Taking the lots together, the following is the result:—

	No. of Plants.	No. of Umbels produced.	No. of Capsules produced.	Weight of seed in grains.
Short-styled Cowslips	9	33	199	83
Long-styled Cowslips	13	51	261	91

If we reduce these elements for comparison to similar terms, we have—

	No. of Plants.	Weight of seed in grains.	No. of Umbels.	Weight of seed.	No. of Capsules.	Weight of seed in grains.
Short-styled Cowslips	10	92	100	251	100	41
Long-styled Cowslips	10	70	100	178	100	34

So that, by all the standards of comparison, the short-styled are the most fertile; if we take the number of umbels (which is the fairest standard, for large and small plants are thus equalized), the short-styled plants produce more seed than the long-styled, in the proportion of four to three.

In 1861 I tried the result in a fuller and fairer manner. I transplanted in the previous autumn a number of wild plants into a large bed in my garden, treating them all alike; the result was—

	No. of Plants.	No. of Umbels.	Weight of seed in grains.
Short-styled Cowslips ...	47	173	745
Long-styled Cowslips ...	58	208	692

These figures, reduced as before, give the following proportions:—

	Number of Plants.	Weight of seed in grains.	Number of Umbels.	Weight of seed in grains.
Short-styled Cowslips ...	100	1585	100	430
Long-styled Cowslips ...	100	1093	100	332

The season was much better this year than the last, and the plants grew in good soil, instead of in a shady wood or struggling with other plants in the open field; consequently the actual produce of seed was considerably greater. Nevertheless we have the same relative result; for the short-styled plants produced more seed than the long-styled in the proportion of three to two; but if we take the fairest standard of comparison, namely, the number of umbels, the excess is, as in the former case, as four to three.

I marked also some Primroses, all growing together under the same conditions; and we here see the product:—

	No. of Plants.	Total No. of Capsules.	Good Capsules.	Weight of seed in grains.	Or by Calculation:	Good Capsules.	Weight of seed.
Short-styled Primroses	8	49	40	16		100	40
Long-styled Primroses	9	68	50	10		100	20

The number of Primrose plants tried was hardly sufficient, and the season was bad; but we here again see (excluding the capsules which contained no seed) the same result in a still more marked manner, for the short-styled plants were twice as productive of seed as the long-styled plants.

I had, of course, no means of ascertaining the relative fertility of the two forms of the Chinese Primrose in a natural condition, and the result of artificial fertilization can hardly be trusted; but sixteen capsules from long-styled flowers, properly fertilized, produce 9·3 grains' weight of seed, whereas eight capsules of short-styled flowers produced 6·1 grains; so that if the same number, namely, 16 of the latter, had been fertilized, the weight of seed would have been 12·2, which would have been nearly in the proportion of four to three, as in Cowslips.

Looking to the trials made during two successive years on the large number of Cowslips, and on these facts with regard to common Primroses and Chinese Primroses, we may safely conclude that the short-styled forms in these species are more productive

than the long-styled forms; consequently the anticipation that the plants having largely developed pistils with rougher stigmas, and having shorter stamens with smaller pollen-grains, would prove to be more feminine in their nature is exactly the reverse of the truth. If the species of *Primula* are tending to become dioicous, which possibly may be the case, the future hypothetical females would have short pistils, and the males would have short stamens; but this tendency is accompanied, as we shall presently see, by other conditions of the generative system of a much more singular nature. Anyhow, the possibility of a plant thus becoming dioicous by slow degrees is worthy of notice, as the fact would so easily escape observation.

In 1860 I found that a few umbels of both long-styled and short-styled Cowslips, which were covered by a net, did not produce seed, though other umbels on the same plants, artificially fertilized, produced an abundance of seed; and this fact shows that the mere covering in itself was not injurious. Accordingly, in 1861 I covered up under a similar net several plants just before they opened their flowers; these turned out as follows:—

	No. of Plants.	No. of Umbels produced.	Product of Seed.
Short-styled	6	24	1·3 grains, or 50 seeds.
Long-styled	18	74	Not one seed.

Judging from the exposed plants which grew all round in the same bed, and had been treated in every way exactly the same, except that they were exposed to the visits of insects, the six short-styled plants ought to have produced 92 grains' weight of seed instead of only 1·3; and the eighteen long-styled plants, which produced not one seed, ought to have produced above 200 grains' weight. The production of the 1·3 grain of seed in the smaller lot was probably due to the action of Thrips or some minute insect. This evidence is sufficient, but I may add that ten pots of Polyanthuses and Cowslips of both forms, protected from insects in my greenhouse, did not set one pod, though artificially fertilized flowers in other pots produced an abundance. So we see that the visits of insects are absolutely necessary to the fertilization of Cowslips. As the exposed plants produced an abundance of seed, the tendency to a dioicous condition, previously remarked on, might have been safely carried on, as we see that there is an effect-

ive agency already at work which would have carried pollen from one sex to the other.

What insects habitually visit Cowslips, as is absolutely necessary for their regular fertility, I do not know. I have often watched them, but perhaps not long enough; and only four times I have seen Humble-bees visiting them. One of these bees was gathering pollen from short-styled flowers alone, another had bitten holes through the corolla; and neither of these would have been effective in the act of fertilization: two others were sucking long-styled plants. I have watched Primroses more attentively during several years, and have never seen an insect visit them; yet from their close similarity in all essential respects to Cowslips, there can hardly be a doubt that they require the visits of insects. Hence I am led to suppose that both Primroses and Cowslips are visited by moths. All the species which I have examined secrete plenty of nectar.

In *Primula Sinensis*, when protected from insects and not artificially fertilized, the case is somewhat, but not materially, different. Five short-styled plants produced up to a given period 116 flowers, which set only seven capsules, whereas twelve other flowers on the same plants artificially fertilized set ten capsules. Five long-styled plants produced 147 flowers, and set sixty-two capsules; so that this form, relatively to the other, sets a far greater number of capsules: yet the long-styled protected flowers do not set nearly so well as when artificially fertilized; for out of forty-four flowers thus treated, thirty-eight set. These remarks apply only to the early setting of the capsules, many of which did not continue swelling. With respect to the product of seed, seven protected short-styled plants, which bore about 160 flowers, produced only half a grain of seed; they ought to have produced 120 grains: so that the short-styled plants, when protected from insects, are nearly as sterile as Cowslips. Thirteen long-styled plants, which bore about 380 flowers, and which as we have seen set many more capsules, produced 25·9 grains of seed; they ought to have produced about 220 grains in weight: so that although far less fertile than the artificially fertilized flowers, yet the long-styled *P. Sinensis*, when protected from insects, is nearly twenty-four times as fertile as the short-styled when protected from insects. The cause of this difference is, that when the corolla of the long styled plants falls off, the short stamens near the bottom of the tube are necessarily dragged over the stigma and leave pollen on it, as I saw by hastening the fall of nearly withered flowers; whereas in the short-styled flowers, the stamens are seated at the mouth of the corolla,

and in falling off do not brush over the lowly seated stigma. In the Cowslip the corolla does not fall off; and both long-styled and short-styled plants are equally sterile when protected from insects. It is a rather curious case, that the falling of the corolla, or its remaining attached when withered, might have a considerable influence on the numbers of a plant, during a year unfavourable to the visits of the proper insects.

In three short-styled plants of *Primula auricula*, protected from insects, the flowers which I fertilized produced seed, but those which were not touched produced none.

In all the species of *Primula* the pollen readily coheres to any object. In all that I have observed, though the stamens and pistils differ in length relatively to each other in the different species, yet, in the two forms of the same species, the stigma of the one form stands at exactly the same height with respect to the corolla as the anthers of the other form. If the proboscis of a dead Humble-bee, or thick bristle, or rough needle be pushed down the corolla, first of one form, and then of the other, as an insect would do in visiting the two mingled forms, it will be found that pollen from the long-stamened form will adhere round the base of the proboscis, and will be left with certainty on the stigma of the long-styled form; pollen from the short stamens of the long-styled form will also adhere a little above the tip of the proboscis, and some will generally be left on the stigma of the other form. Thus pollen will be carried reciprocally from one form to the other. In withdrawing the proboscis from the long-styled form, with pollen adhering near the tip, there will be a good chance of some being left on the flower's own stigma, in which case there will be self-fertilization; but this by no means always occurs. In the short-styled form, on the other hand (and it is important to remember this), in inserting the proboscis between the anthers situated at the mouth of the corolla, pollen, as I repeatedly found, is almost invariably carried down and left on the flower's own stigma. Moreover minute insects, such as Thrips, numbers of which I have observed in Primrose flowers thickly dusted with pollen, could not fail often to cause self-fertilization. We positively know that the visits of large insects are necessary to the fertilization of the species of *Primula*; and we may infer from the facts just given that these visits would carry pollen reciprocally from one form to the other, and would likewise *tend* to cause self-fertilization, more especially in the short-styled (*i. e.* long-stamened) form.

These observations led me to test the potency of the two pol-

lens with respect to the two stigmas in *P. veris, Sinensis,* and *auricula.* In each species four crosses can be tried; namely, the stigma of the long-styled by its own-form pollen and by that of the short-styled, and the stigma of the short-styled by its own-form pollen and by that of the other form. It is necessary to use and remember two new terms for these crosses: when the long- and the short-styled stigmas are fertilized by their own-form pollen the union is said to be "homomorphic;" when the long-styled and short-styled stigmas are fertilized by the pollen of the other form, the union is "heteromorphic." I speak of the "own-form pollen," because in the following homomorphic unions, in order to make the experiment perfectly fair, I never placed the pollen of the same flower on its own stigma, but, to avoid the possible ill effects of close interbreeding, I always used the pollen from another plant of the same form. In the following experiments all the plants were treated in exactly the same manner, and were carefully protected from insects as far as that is possible. I performed every manipulation myself, and weighed the seed in a chemical balance. Some of the capsules contained no seed, or only two or three, and these are excluded in the column marked "good pods." First for *P. Sinensis,* as the simplest case.

Primula Sinensis.—Table I.

	Number of flowers fertilized.	Total number of pods produced.	Number of good pods.	Weight of seed in grains.	By Calculation. Good Pods. / Weight of seed in grains.
Long-styled by own-form pollen (homomorphic union)	20	18	13	5·9	or as 100 to 45
Long-styled by pollen of short-styled (heteromorphic union)...	24	18	16	9·3	or as 100 to 58
Short-styled by own-form pollen (homomorphic union)	7	5	4	0·9	or as 100 to 22
Short-styled by pollen of long-styled (heteromorphic union)...	8	8	8	6·1	or as 100 to 76
Summary:					
The two homomorphic unions	27	23	17	6·8	
The two heteromorphic unions	32	26	24	15·4	

For the sake of comparison, we may reduce these latter figures as follows:—

	Number of flowers fertilized.	Number of good pods.	Weight of seed in grains.	Number of good pods.	Weight of seed in grains.
The two homomorphic unions	100	63	25	100	40
The two heteromorphic unions	100	75	48	100	64

In the first part of the upper table, the number of flowers fertilized and the simple result is shown; and at the right hand, for the sake of comparison, the calculated product of the weight of seed from 100 good pods of each of the four unions is given; showing that in each case the heteromorphic union is more fertile than the homomorphic union. Beneath we have a simple summary of the two homomorphic and the two heteromorphic unions. And lastly, for the sake of comparison, a calculation has been made from this summary; first, assuming that 100 flowers of both kinds of unions were fertilized; and then to the right hand, assuming that 100 good pods were produced from both unions. If we compare the result, we see that the flowers of the two heteromorphic unions produced a greater number of good pods, and a greater weight of seed, than the flowers of the two homomorphic unions; and again (and this is the fairest element of comparison, for accidents are thus almost eliminated), that the good pods from the two heteromorphic unions yielded more seed, in about the proportion of three to two, than those from the two homomorphic unions. The difference in weight from 100 capsules of the two forms is 24 grains, and this is equal to at least 1200 seeds.

Beneath we have Table II. of *P. veris*, or the Cowslip. The upper part is exactly the same as in the Table of *P. Sinensis*, and we see in each case that the heteromorphic is more fertile than the homomorphic union. The calculated results from the summary of the two homomorphic and the two heteromorphic unions are more complex than with the last species, as I wished to show that, however we proceed, the general result is the same. We see that the assumed hundred flowers, heteromorphically fertilized by the pollen of the other forms, yielded more capsules, more good capsules, and a greater weight of seed; but I rely little on this, as some whole umbels perished after being fertilized. The fairest element of comparison is to take the good capsules alone; and we here see that the 100 from the two heteromorphic unions yielded seed which in weight was as 54 to 35 from the 100 good capsules

of the two homomorphic unions,—that is, nearly as three to two, as in the Chinese Primrose.

Primula veris.—Table II.

	Number of flowers fertilized.	Total number of pods produced.	Number of good pods.	Weight of seed in grains.	By Calculation. Good Pods. { Weight of seed in grains.
Long-styled by own-form pollen (homomorphic union)	20	8	5	2·1	or as 100 to 42
Long-styled by pollen of short-styled (heteromorphic union)...	22	15	14	8·8	or as 100 to 62
Short-styled by own-form pollen (homomorphic union)	15	8	6	1·8	or as 100 to 30
Short-styled by pollen of long-styled (heteromorphic union)...	13	12	11	4·9	or as 100 to 44
Summary:					
The two homomorphic unions	35	16	11	3·9	
The two heteromorphic unions	35	27	25	13·7	

For the sake of comparison, we may reduce these figures as follows:—

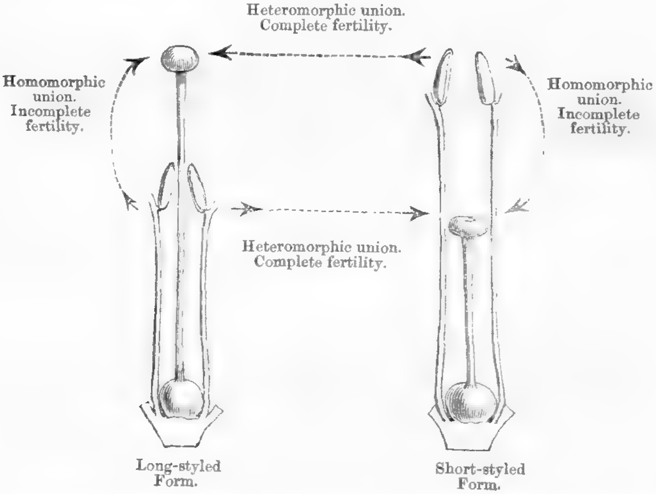
	Number of flowers fertilized.	Total number of pods produced.	Number of good pods.	Weight of seed in grains.	Total number of pods produced.	Weight of seed in grains.	Number of good pods.	Weight of seed in grains.
The two homomorphic unions	100	45	31	11	100	24	100	35
The two heteromorphic unions	100	77	71	39	100	50	100	54

With *P. auricula* I was unfortunate; my few seedlings, except one poor plant, all came up short-styled; and of these plants several died or became sick, owing to the hot weather and the difficulty of excluding insects and ventilating the corner of my greenhouse enclosed with net. I finally got only two pods from one union, and three from the other. The result is given in the following table; and, though worth little, we here again see that the heteromorphic are far more fertile than the homomorphic unions.

Primula auricula.—Table III.

	Total number of pods produced.	Number of good pods.	Weight of seed in grains	Good Pods. } Weight of seed in grains.
Short-styled by own-form pollen (homomorphic union) ..	2	1	0·12	or as 100 to 12
Short styled by pollen of long-styled (heteromorphic union)	3	3	1·50	or as 100 to 50

Whoever will study these three tables, which give the result of 134 flowers carefully fertilized and protected, will, I think, be convinced that in these three species of *Primula* the so-called heteromorphic unions are more fertile than the homomorphic unions. For the sake of clearness, the general result is given in the following diagram, in which the dotted lines with arrows represent how in the four unions pollen has been applied.



We here have a case new, as far as I know, in the animal and vegetable kingdoms. We see the species of *Primula* divided into two sets or bodies, which cannot be called distinct sexes, for both are hermaphrodites; yet they are to a certain extent sexually distinct, for they require for perfect fertility reciprocal union. They might perhaps be called sub-dioicous hermaphrodites. As quadrupeds are divided into two nearly equal bodies of different sexes, so here we have two bodies, approximately equal in number,

differing in their sexual powers and related to each other like males and females. There are many hermaphrodite animals which cannot fertilize themselves, but must unite with another hermaphrodite: so it is with numerous plants; for the pollen is often mature and shed, or is mechanically protruded, before the flower's own stigma is ready; so that these hermaphrodite flowers absolutely require for their sexual union the presence of another hermaphrodite. But in *Primula* there is this wide difference, that one individual Cowslip, for instance, though it can with mechanical aid imperfectly fertilize itself, for full fertility must unite with another individual; but it cannot unite with any individual in the same manner as an hermaphrodite Snail or Earth-worm can unite with any other one Snail or Earth-worm; but one form of the Cowslip, to be perfectly fertile, must unite with one of the other form, just as a male quadruped must and can unite only with a female.

I have spoken of the heteromorphic union in *Primula* as resulting in full fertility; and I am fully justified, for the Cowslips thus fertilized actually gave rather more seed than the truly wild plants —a result which may be attributed to their good treatment and having grown separately. With respect to the lessened fertility of the homomorphic unions, we shall appreciate its degree best by the following facts. Gärtner has estimated the degree of sterility of the union of several distinct species*, in a manner which allows of the strictest comparison with the result of the heteromorphic and homomorphic unions of *Primula*. With *P. veris*, for every hundred seeds yielded by the heteromorphic unions, only sixty-four seeds were yielded by an equal number of good capsules from the homomorphic unions. With *P. Sinensis* the proportion was nearly the same—namely, as 100 to 62. Now Gärtner has shown that, on the calculation of *Verbascum lychnitis* yielding with its own pollen 100 seeds, it yields when fertilized by the pollen of *V. Phœniceum* ninety seeds; by the pollen of *V. nigrum*, sixty-three seeds; by that of *V. blattaria*, sixty-two seeds. So again, *Dianthus barbatus* fertilized by the pollen of *D. superbus* yielded eighty-one seeds, and by the pollen of *D. Japonicus* sixty-six seeds, relatively to the 100 seeds produced by its own pollen. Thus we see—and the fact is highly remarkable—that the homomorphic unions relatively to the heteromorphic unions in *Primula* are more sterile than the crosses between several distinct species relatively to the pure union of those species.

The meaning or use of the existence in *Primula* of the two

* Versuche über die Bastarderzeugung, 1849, s. 216.

forms in about equal numbers, with their pollen adapted for reciprocal union, is tolerably plain; namely, to favour the intercrossing of distinct individuals. With plants there are innumerable contrivances for this end; and no one will understand the final cause of the structure of many flowers without attending to this point. I have already shown that the relative heights of the anthers and stigmas in the two forms lead to insects leaving the pollen of the one form on the stigma of the other; but, at the same time, there will be a strong probability of the flower's own pollen being likewise placed on the stigma. It is perfectly well known that if the pollen of several closely allied species be placed on the stigma of a distinct species, and at the same time, or even subsequently, its own pollen be placed on the stigma, this will entirely destroy the simultaneous or previous action of the foreign pollen. So again if the pollen of several varieties, including the plant's own pollen, be placed on the stigma, one or more of the varieties will take the lead and obliterate the effect of the others: but I have not space here to give the facts on which this conclusion is grounded. Hence we may infer as highly probable that, in *Primula*, the heteromorphic pollen which we know to be so much the most effective would obliterate the action of the homomorphic pollen when left on the flower's own stigma by insects; and thus we see how potent the dimorphic condition of the pollen in *Primula* will be in favouring the intercrossing of distinct individuals. The two forms, though both sexes are present in each, are in fact dioicous or unisexual. Whatever advantage there may be in the separation of the sexes, towards which we see so frequent a tendency throughout nature, this advantage has been here so far gained, that the one form is fertilized by the other, and conversely; and this is effected by the pollen of each form having less potency than that of the other on its own stigma.

Bearing on this view of the final cause of the dimorphism of the *Primulas*, there is another curious point. If we look at the right-hand figures of the four first lines in the previous tables of *P. Sinensis* and *veris*, we shall see that one of the homomorphic unions, namely, the short-styled by its own-form pollen, is considerably more sterile than the other; and in *P. auricula*, though here there is no other homomorphic union as a standard of comparison, this union is likewise excessively sterile. That the fertility of this union is really less in a marked degree than in the other three unions, we have an independent proof in the seeds germinating less perfectly and much more slowly than those from the other unions.

This fact is the more remarkable, because we have clearly seen that the short-styled form in the Cowslip in a state of nature is the most productive of seed. This form bears its anthers close together at the mouth of the corolla, and I observed long before I had ascertained the relative fertility of the four unions, in passing the proboscis of a dead Humble-bee or bristle down the the corolla, that in this form the flower's own pollen was almost certain to be left on its own stigma; and, as I wrote down at the time, the chance of self-fertilization is much stronger in this than in the other form. On this view we can at once understand the good of the pollen of the short-styled form, relatively to its own stigma, being the most sterile; for this sterility would be the most requisite to check self-fertilization, or to favour intercrossing. Hence, also, it would appear that there are four grades of fertility from the four possible unions in *Primula*; of the two homomorphic unions, as we have just seen, one is considerably more sterile than the other. In the wild state we know that the short-styled plants are more fertile than the long-styled; and we may infer as almost certain, that in the wild state, when the flowers are visited by insects, as is absolutely necessary for the production of seed, and when pollen is freely carried from one form to the other, that the unions are heteromorphic; if so, there are two degrees of fertility in the heteromorphic unions, making altogether four grades of fertility.

Two or three other points deserve a passing notice. The question whether the Primrose and Cowslip (*P. vulgaris* and *veris*) are distinct species or varieties has been more disputed and experimented on than in any other plant. But as we now know that the visits of insects are indispensable to the fertilization of these plants, and that in all probability the heteromorphic pollen of a Primrose would be prepotent on the stigma of a Cowslip over the homomorphic pollen of a Cowslip, the numerous experiments which have been made, showing that Oxlips appear amongst the seedlings of Cowslips, cannot be trusted, as the parent plants do not appear to have been carefully protected from insects*. I am far from wishing to affirm that pure Cowslips will not produce Ox-

* Mr. Sidebotham (Phytologist, vol. iii. pp. 703–5) states that he protected his plants from crossing; but as he gives in detail all the precautions which he took, and says nothing about artificial fertilization, we may conclude that he did not fertilize his plants. As he raised very numerous seedlings, he would have had to fertilize many flowers, if they had been really well guarded against the visits of insects. Hence I conclude that his results are not worthy of trust.

lips, but further experiments are absolutely necessary. We may also suspect that the fact noticed by florists*, that the varieties of the Polyanthus never come true from seed, may be *in part* due to their habitually crossing with other varieties of the Polyanthus.

The simple fact of two individuals of the same undoubted species, when homomorphically united, being as sterile as are many distinct species when crossed, will surprise those who look at sterility as a special endowment to keep created species distinct. Hybridizers have shown† that individual plants of the same species vary in their sexual powers, so far that one individual will unite more readily than another individual of the same species with a distinct species. Seeing that we thus have a groundwork of variability in sexual power, and seeing that sterility of a peculiar kind has been acquired by the species of *Primula* to favour intercrossing, those who believe in the slow modification of specific forms will naturally ask themselves whether sterility may not have been slowly acquired for a distinct object, namely, to prevent two forms, whilst being fitted for distinct lines of life, becoming blended by marriage, and thus less well adapted for their new habits of life. But many great difficulties would remain, even if this view could be maintained.

Whether or not the dimorphic condition of the *Primulæ* has any bearing on other points in natural history, it is valuable as showing how nature strives, if I may so express myself, to favour the sexual union of distinct individuals of the same species. The resources of nature are illimitable; and we know not why the species of *Primula* should have acquired this novel and curious aid for checking continued self-fertilization through the division of the individuals into two bodies of hermaphrodites with different sexual powers, instead of by the more common method of the separation of the sexes, or by the maturity of the male and female elements at different periods, or by other such contrivances. Nor do we know why nature should thus strive after the intercrossing of distinct individuals. We do not even in the least know the final cause of sexuality; why new beings should be produced by the union of the two sexual elements, instead of by a process of parthenogenesis. When we look to the state in which young mammals and birds are born, we can at least see that the object gained is

* Mr. D. Beaton, in 'Journal of Horticulture,' May 28, 1861, pp. 154, 244.

† Gärtner, Bastarderzeugung, s. 165.

not, as has sometimes been maintained, mere dissemination. The whole subject is as yet hidden in darkness.

I will now only add that cases of dimorphism, like that of *Primula*, seem to be far from rare in the vegetable kingdom, though they have been little attended to. A large and important class of analogous facts will probably soon be discovered. Professor Asa Gray* informs me, that he and Dr. Torrey have described several Rubiaceous genera, in which some plants have exserted stamens, and others exserted pistils. "Mitchella offers an interesting instance of this structure from its relationship, through *Nertera,* to *Coprosma,* one of the few diœcious genera of *Rubiaceæ,* and in which the stamens are elongated in the male flowers and the styles in the females." The long-styled hermaphrodite flowers of Mitchella would probably be found more productive of seed than the short-styled; in the same way, but in a reversed manner, as in *Primula,* the short-styled flowers are more productive than the long-styled; from which fact I inferred that, if *Primula* were to become diœcious, the females would have short pistils and the males short stamens, these being the corresponding organs necessary for a heteromorphic union with full fertility. In the diœcious *Coprosma,* on the other hand, the females have long pistils, and the males have long stamens. These facts probably show us the stages by which a diœcious condition has been acquired by many plants.

Prof. A. Gray also informs me that another Rubiaceous genus (*Knoxia*) in India has been described by Dr. Wight, with a similar structure; and this, I am told, is the case with *Cinchona.* Several species of North American *Plantago* are dimorphic, as is *Rhamnus lanceolatus,* as far as its female organs are concerned. In the *Boragineæ,* Dr. Torrey has observed a strongly marked instance in *Amsinckia spectabilis*: in some dried flowers sent me by Prof. Gray, I find that the pistil in the one form is more than twice as long as in the other, with a corresponding difference in the length of the stamens; in the short-styled flowers the grains of pollen, as in *Primula,* apparently are larger, in the proportion of nine to seven, than in the long-styled flowers, which have the short stamens; but the difference can hardly be determined with safety in dried flowers. In *Mertensia alpina,* another member of

* See also Prof. Asa Gray's 'Manual of the Botany of the N. United States,' 1856, p. 171. For *Plantago,* see p. 269.

the *Boragineæ*, Prof. Gray finds a new and inexplicable case,—namely, some specimens with the stamens and pistil sub-exserted, and other specimens with *both* organs seated low down the tube of the corolla. Dr. Torrey and Prof. Gray have designated all such plants as "diœciously dimorphous." In the *Labiatæ*, Mr. Bentham informs me that several species of *Ægiphyla*, and some of *Mentha*, are dimorphic like *Primula*. The case of *Thymus* is different, as I know from my own observations; but I will not here enlarge on this genus. Again, as I hear from Mr. Bentham, numerous species of *Oxalis* are similarly dimorphic. I can add the genus *Linum*. So that we already know of species (generally several in the same genus) having distinct dimorphic individuals, as far as structure is concerned, however it may prove in function, in no less than eight natural orders.

With respect to *Linum*, I will not here enter on details, as I intend to try further experiments next summer; but I may state, that I observed many years ago two forms in *Linum flavum*, with both the pistils and stamens differing in length. In *Linum grandiflorum* there are likewise two forms which present no difference in their male organs, but the pistil and stigmatic surfaces are much longer in the one form than in the other. The short-styled form, I have good reason to believe, is highly fertile with its own pollen; whether it be more fertile with the pollen of the long-styled form, I cannot at present say. The long-styled form, on the other hand, is quite sterile with its own pollen: several plants grew in my garden, remote from the short-styled plants; their stigmas were coloured blue with their own pollen; but although they produced a vast number of flowers, they did not produce a single seed-capsule. It seemed a hopeless experiment; but I had so much confidence from my trials on *Primula*, that I put a little pollen from the short-styled plants on the stigmas (already blue with their own pollen) of twelve flowers on two of the long-styled plants. From these twelve flowers I got eight remarkably fine seed-capsules; the other flowers not producing a single capsule. The existence of plants in full health, and capable of bearing seed, on which their own pollen produces no more effect than the pollen of a plant of a different order, or than so much inorganic dust, is one of the most surprising facts which I have ever observed.

organs are almost concealed by the spathe and bracts. Its nearest known ally is probably *H. rostrata*, Ruiz and Pavon, a native of Peru. Dr. Anthoine desires that this noble plant should bear the name of the Empress of Russia, which I have therefore attached to it.

HELICONIA MARIÆ, *Hook. f.* Foliorum vaginis truncum elatum efformantibus, lamina oblonga petiolata ampla, spicis longe pedunculatis pendulis, spathis crebre dense disticho-imbricatis rachin omnino velantibus late ovato-cymbiformibus recurvis obtusis, floribus bracteis inclusis glabratis.

Hab. Betami on the Sinu River (lat. 8° N.), State of Bolivar, in New Granada (*Dr. A. Anthoine*).

Truncus 3–4 metr., cum foliis 6 metr., etiam 10–15 centimetr., lævis, viridi-purpureus (*Anth.*). *Folia* oblonga v. lineari-oblonga, obtusa, 3–4 ped. longa, petiolo æquilonga, viridia. *Pedunculus* crass. digiti, curvus, glaber, siccus flexuosus, teres, intus vasibus mollibus farctus. *Spicæ* 1½ ped. longæ, 3–4 poll. latæ, lineares, obtusæ, compressæ. *Spathæ* 60–80, dense imbricatæ, reflexæ, valde concavæ, late ovato-cymbiformes, glabræ v. pubescentes, lateribus erectis, basin versus subcordatæ, marginibus undulatis, apice obtusiusculæ; infimæ rostratæ; inferiores 1–2 distantes, 4–5 unc. longæ, rachin pubescentem non tegentibus; cæteræ 2–2½ unc. longæ, rachin velantes; superiores inferiores amplectentes. *Flores* rubri (*Anth.*), in spatha singula 15–20, bracteis lineari-lanceolatis glabriusculis inclusi, receptaculo brevissimo in axilla spathæ inserti; apicibus perianthii tantum exsertis. *Bracteæ* albæ, spatha breviores, ovato-lanceolatæ, basi concavæ, exteriores vacuæ. *Pedicelli* ½″ longi, crassiusculi, villosuli, compressi. *Ovarium* trigonum. *Perianthium* 1″ long., foliolis extus subtomentosis. *Stylus* apice incurvus. *Antheræ* inclusæ. *Drupa* cærulea (*Anth.*), 3-cocca; coccis oblongis, compressis, basi antice fovea cupulæformi notatis, subrugosis, osseis, intus subrugosis. *Semen* erectum; testa membranacea, raphe annulari circumdata. *Albumen* subfarinaceum. *Embryo* axillaris, gracilis, extremitate radiculari paulo crassiore, germinatione foveam cocci perforante.

On the existence of two forms, and on their reciprocal sexual relation, in several species of the genus *Linum*. By CHARLES DARWIN, M.A., F.R.S., F.L.S., &c.

[Read February 5, 1863.]

THE crimson *Linum grandiflorum* presents two forms, occurring in about equal numbers, which differ little in structure, but greatly in function. The foliage, corolla, stamens, and pollen (examined

Mo. Bot. Garden,
1896.

dry, and distended with water) are alike in both forms. The difference is confined to the pistil: in the one form, which I will call "short-styled," the column formed by the united styles, and the short stigmas, together is about half the length of the whole pistil in the other and "long-styled" form. A more important distinction is, that the five stigmas in the short-styled form diverge greatly from each other and pass out between the filaments of the stamens, and thus lie within the tube of the corolla. In the long-styled form the elongated stigmas stand nearly upright, and alternate with the anthers. In this latter form the length of the stigmas varies considerably, their upper extremities projecting even a little above the anthers, or reaching up only to about their middle. Nevertheless there is never the slightest difficulty in distinguishing between the two forms; for, besides the difference in divergence, the stigmas of the short-styled form never reach even to the bases of the anthers. In the short-styled, the papillæ on the stigmatic surfaces are shorter, darker-coloured, and more crowded together than in the long-styled form: but these differences seem due merely to the shortening of the stigma; for in the varieties of the long-styled form with shorter stigmas, the papillæ are more crowded and darker-coloured than in those with the longer stigmas. Considering the slight and variable differences between the two forms of this *Linum*, it is not surprising that they have been hitherto overlooked.

In 1861 I had eleven plants growing in my garden, eight of which were long-styled, and only three short-styled. Two very fine long-styled plants grew in a bed a hundred yards off, and separated from the others by a screen of evergreens. I marked twelve flowers, and put on their stigmas a little pollen from the short-styled plants. The pollen of the two forms is, as stated, identical in appearance; the stigmas of the long-styled flowers were already thickly covered with their own pollen—so thickly that I could not find one bare stigma; and it was late in the season, namely, September 15th. Altogether, to expect any result from this trial seemed almost childish. From my experiments, however, on *Primula*, which have been laid before this Society ('Journal,' vol. vi. p. 77), I had faith, and did not hesitate to make the trial, but certainly I did not anticipate the full result. The germens of these twelve flowers all swelled, and ultimately six fine capsules (the seed of which germinated this year) and two poor capsules were produced; only four capsules shanked off. These

two plants produced, before and after and at the time of the trial, a vast number of flowers, but the germens of not even one swelled. All these flowers, though their stigmas were so densely covered with their own pollen, were absolutely barren.

The nine other plants, six long-styled and three short-styled, grew in the beds of the same flower-garden. Four of the long-styled produced no seed-capsules; one produced two; but the remaining long-styled plant grew so close to a short-styled plant that their branches touched, and this produced twelve capsules, but they were poor. The case was different with the short-styled plants. The plant which grew in juxtaposition with the long-styled plant produced ninety-four imperfectly fertilized capsules containing a multitude of bad seeds, with a moderate number of good seeds. The two other short-styled plants grew in a single clump, and were very small, being partly smothered by other plants; they did not stand very close to any long-styled plants, yet they yielded together nineteen capsules. These facts seem to show that the short-styled plants are far more fertile with their own pollen than the long-styled. We shall immediately see that this is the case in a slight degree. But I suspect that in this instance the difference in fertility between the two forms was in part due to a distinct cause. I repeatedly watched the flowers, and only once saw a humble-bee momentarily alight on one, and then fly away, as if it were not to its taste. If bees had visited the several plants, there cannot be a doubt that the four long-styled plants which did not produce a single capsule would have borne an abundance. But several times I saw small diptera sucking the flowers; and these insects, though not visiting the flowers with anything like the regularity of bees, would carry a little pollen from one form to the other, especially when growing close together; and the stigmas of the short-styled plants, diverging within the tube of the corolla, would be more likely than the upright stigmas of the long-styled to receive a small quantity of pollen when brought by small insects. From the much greater number of long-styled than of short-styled flowers in the garden, evidently the short-styled would be more likely to receive some pollen from the long-styled, than the long-styled from the short-styled.

In 1862 I raised thirty-four plants of this *Linum* in a hotbed; and these consisted of seventeen long-styled and seventeen short-styled forms. Seed sown later in the flower-garden yielded seventeen long-styled and twelve short-styled forms. These facts justify

the statement that the two forms are produced in about equal numbers. The first thirty-four plants were kept under a net which excluded insects. I fertilized heteromorphically fourteen long-styled flowers with pollen from the short-styled, and got eleven fine seed-capsules; these contained on an average 8·6 seeds per capsule, but only 5·6 were apparently good. It may be well to state that ten seeds is the maximum possible production for a capsule, and that our climate cannot be very favourable to this North-African plant. On three occasions I fertilized homomorphically the stigmas of altogether nearly a hundred flowers (but did not separately mark them) with their own pollen, but taken from separate plants, so as to prevent any possible ill effects from close interbreeding; and many other flowers were produced, which, as before stated, would get plenty of their own individual pollen; yet from all these flowers, borne by the seventeen long-styled plants, only three capsules were produced; one of these included no seed, and the other two together gave only five good seeds. Nor do I feel at all sure that this miserable product of the two half-fertile capsules from the seventeen plants, each of which must have produced at least fifty or sixty flowers, is really the result of their fertilization by their own pollen; for I made a great mistake in keeping the two forms under the same net, with their branches often interlocking, and it is surprising that a greater number of flowers were not accidentally fertilized.

Of the short-styled flowers I fertilized heteromorphically twelve with the pollen of the long-styled (and to make sure of the result I previously castrated the majority), and obtained seven fine seed-capsules. These included an average of 7·6 seeds, but of apparently good seed only 4·3 per capsule. At three separate times I fertilized homomorphically nearly a hundred flowers with their own-form pollen, taken from separate plants; and numerous other flowers were produced, many of which must have received their own pollen. From all these flowers borne on the seventeen plants, only fifteen capsules were produced, of which only eleven contained any good seed, on an average 4·2 per capsule. As remarked in the case of the long-styled plants, some even of these capsules were perhaps the product of a little pollen accidentally fallen from the flowers of the other form. Nevertheless the short-styled plants seem to be slightly more fertile with their own pollen, in the proportion of fifteen capsules to three, than the long-styled: the real proportional excess in fertility is probably a little greater, as the short-styled flowers, when not disturbed, do

not so surely receive their own pollen as do the long-styled. The greater self-fertility of the short-styled flowers was, as we have seen, also shown by the plants left to themselves, and but sparingly visited by insects, in the flower-garden in 1861, and likewise by those raised in 1862.

The absolute sterility (judging from the experiments of 1861, and which is hardly contradicted by those of 1862) of the long-styled plants with their own-form pollen led me to examine into its apparent cause; and the result is so curious that it will be worth while to give most of the experiments in detail. These experiments were tried on fresh plants, grown in pots and brought successively into the house.

First. I placed pollen from a short-styled flower on the five stigmas of a long-styled plant, and after thirty hours found them deeply penetrated by a multitude of pollen-tubes, far too numerous to be counted; the stigmas had become discoloured and twisted. I repeated this experiment on another flower, and in 18 hours found the stigmas penetrated by a multitude of long pollen-tubes. All this is what might have been expected, as this is a fertile or heteromorphic union. I likewise tried the converse experiment, and placed pollen from a long-styled flower on the stigmas of a short-styled flower, and in 24 hours found the stigmas discoloured, twisted, and penetrated by numerous pollen-tubes; and this, again, is what might have been expected, as this is a fertile or heteromorphic union.

Secondly. I placed pollen of a long-styled flower on all five stigmas of a long-styled flower on a separate plant: after 19 hours I rigorously dissected the stigmas, and found only a single pollen-grain which had emitted a very short tube. To make sure that the pollen was good, I took in this case, and in most other cases, pollen either from actually the same anther or from the same flower, and proved it to be good by placing it on the stigma of a short-styled plant, and seeing numerous pollen-tubes emitted.

Thirdly. Repeated last experiment, and placed own-form pollen on all five stigmas of a long-styled flower; and, after 19½ hours, not one single grain had emitted its tube.

Fourthly. Repeated the experiment, with the same result after 24 hours.

Fifthly. Repeated last experiment, and, after leaving pollen on for 19 hours, put an additional quantity of own-form pollen on all five stigmas. After an interval of exactly three whole days, I rigorously examined the stigmas, which, instead of being dis-

coloured and twisted, were straight and fresh-coloured; and only one grain had emitted quite a short tube, which could be drawn out of the stigmatic tissue without being ruptured.

The following experiments are more striking:—

Sixthly. I placed own-form pollen on three of the stigmas of a long-styled flower, and pollen from a short-styled flower on the other two stigmas. After 22 hours these two stigmas were discoloured, and slightly twisted, and penetrated by the tubes of numerous pollen-grains: the other three stigmas, covered with their own-form pollen, were fresh, and all the pollen-grains were loose; but I did not dissect the whole stigma rigorously.

Seventhly. Experiment repeated in the same manner, with the same result.

Eighthly. Experiment repeated, but the stigmas were carefully examined after an interval of only $5\frac{1}{2}$ hours. The two stigmas with pollen from a short-styled flower were penetrated by innumerable tubes; but these were as yet short, and the stigmas themselves were not at all discoloured. The three stigmas covered with their own-form pollen were not penetrated by a single pollen-tube.

Ninthly. Put pollen of short-styled on one stigma, and own-form pollen on the other four stigmas; after 24 hours, found the one stigma somewhat discoloured, and twisted, and penetrated by many long tubes: the other four stigmas were quite straight and fresh; but on dissecting their whole lengths I found that three pollen-grains had protruded quite short tubes into the tissue.

Tenthly. Repeated the experiment, with the same result after 24 hours, excepting that only two own-form grains had penetrated the stigmatic tissue with their tubes, to a very short depth: the one stigma, which was deeply penetrated by a multitude of tubes from the short-styled pollen, presented a conspicuous difference in comparison with the other four straight and bright pink stigmas, in being much curled, half-shrivelled, and discoloured.

I could add a few other experiments; but those now given amply suffice to show that the pollen-grains of a short-styled flower placed on the stigmas of a long-styled flower emit a multitude of tubes after an interval of from five to six hours, and penetrate the tissue ultimately to a great depth, and that after twenty-four hours the stigmas thus penetrated change colour, become twisted, and appear half-withered. On the other hand, the pollen-grains of the long-styled flowers placed on their own stigmas, after an interval of a day, or even three days, do not emit their tubes, or at most only three or four grains out of a multitude emit their tubes; and these

apparently never penetrate the stigmatic tissue deeply, and the stigmas themselves do not become discoloured and twisted.

This seems to me a remarkable physiological fact. The pollen-grains of the two forms are undistinguishable under the microscope; the stigmas differ only in length, degree of divergence, and in the size, shade of colour, and approximation of their papillæ, these latter differences being variable and apparently simply due to the elongation of the stigma. Yet we plainly see that the two pollens and the two stigmas are widely dissimilar in action—the stigmas of each form being almost powerless on their own pollen, but causing, through some mysterious influence, by simple contact (for I could detect no viscid secretion), the pollen-grains of the opposite form to protrude their tubes. It may be said that the two pollens and the two stigmas by some means mutually recognize each other. Taking fertility as the criterion of distinctness, it is no exaggeration to say that the pollen of the long-styled *Linum grandiflorum* (and conversely of the other form) has been differentiated, with respect to the stigmas of all the flowers of the same form, to a degree corresponding with that of distinct species of the same genus, or even of species of distinct genera.

Linum perenne.—The dimorphism is here more conspicuous, and has been noticed by several authors. In the long-styled form the pistil is nearly twice as long as in short-styled; in the latter the stigmas are smaller and, diverging more, pass out between the filaments of the stamens. I could detect no difference in the size of the stigmatic papillæ; in the long-styled form alone the stigmatic surfaces turn round so as to face the circumference of the flower: but to this point we shall presently return. Differently from what occurs in *L. grandiflorum*, the long-styled flowers have stamens hardly more than half the length of those of the short-styled. The size of the pollen-grains is rather variable; after some doubt, I have come to the conclusion that there is no uniform difference between the pollen of the two forms. The long stamens in the short-styled form project to some height above the corolla, and, apparently from exposure to the light, the filaments are coloured blue. These longer stamens correspond in height with the lower part of the stigmas of the long-styled flowers; and the shorter stamens of the latter form correspond in the same manner in height with the shorter stigmas of the short-styled flowers.

I raised from seed twenty-six plants, which proved to be twelve long-styled and fourteen short-styled. They flowered well, but were not large plants. As I did not expect them to flower so

soon, I did not transplant them, and they unfortunately grew with their branches closely interlocked. All the plants were covered by a net, excepting one of each form. First, of the long-styled flowers, twelve were homomorphically fertilized by their own-form pollen, taken in every case from a separate plant; and not one flower set a seed-capsule: twelve other flowers were heteromorphically fertilized by pollen from short-styled flowers; and they set nine pods, each including on an average seven good seeds: as before, ten seeds is the maximum possible production. Secondly, of the short-styled flowers, twelve were homomorphically fertilized by own-form pollen, and they yielded one capsule, including only three good seeds; twelve other flowers were heteromorphically fertilized by pollen of long-styled flowers, and these produced nine capsules, but one was bad; the eight good capsules contained on an average exactly eight good seeds each.

The many flowers on the eleven long-styled plants under the net, which were not fertilized, produced only three capsules (including 8, 4, and 1 good seeds); whether, owing to the interlocking of the branches, these accidentally received pollen from the other form, I will not pretend to conjecture. The single long-styled plant which was uncovered, and grew close by the uncovered short-styled plant, produced five good pods; but it was a very poor and small plant.

The flowers borne on the thirteen short-styled plants under the net, which were not fertilized, produced twelve capsules (containing 5·6 seeds on average): as some of these capsules were very fine, and five were borne on one twig, I suspect that they had been visited by some minute insect which had accidentally got under the net and had carried pollen from the other form. The one uncovered short-styled plant yielded exactly the same number of capsules, namely, twelve.

From these facts we have some evidence, as in the case of *L. grandiflorum*, that the short-styled plants are in a very slight degree more fertile with their own pollen than are the long-styled plants. And we have the clearest evidence, from the result of the forty-eight flowers artificially fertilized, that the stigmas of each form require pollen from the stamens of corresponding height produced by the opposite form.

In contrast with the case of *L. grandiflorum*, it is a singular fact that the pollen-grains of both forms of *L. perenne* when placed on their own-form stigmas, though not causing fertility, yet emit their tubes; and these tubes I found, after an interval of eighteen

hours, had penetrated the stigmatic tissue, but to what depth I did not ascertain. In this case the inaction of the pollen-grains on their own stigmas must be due either to the tubes not reaching the ovules, or reaching them and not efficiently acting on them. In the case of *Lythrum Salicaria,* which I hope at some future time to lay before the Society, there are three distinct forms, each of which produces two kinds of pollen; but neither pollen, when placed on its own stigma, causes fertility, except occasionally and in a very moderate degree; yet the pollen-tubes in each case freely penetrate the stigmatic tissue.

The plants of *L. perenne* and of *L. grandiflorum* grew, as stated, with their branches interlocked, and with scores of flowers of the two forms close together; they were covered by an open net, through which the wind, when high, passed; and such minute insects as *Thrips* could not, of course, be excluded; yet we have seen that the utmost possible amount of accidental fertilization on seventeen long-styled plants in the one case, and on eleven plants in the other case, was the production, in each, of three poor capsules; so that we may infer that, when the proper insects are excluded, the wind does hardly anything in the way of carrying pollen from plant to plant. I allude to this fact because botanists, in speaking of the fertilization of plants or of the production of hybrids, often refer to the wind or to insects as if the alternative were indifferent. This view, according to my experience, is entirely erroneous. When the wind is the agent in carrying pollen, either from one separated sex to the other, or from hermaphrodite to hermaphrodite (which latter case seems to be almost equally important for the ultimate welfare of the species, though occurring perhaps only at long intervals of time), we can recognize structure as manifestly adapted to the action of the wind as to that of insects when they are the carriers. We see adaptation to the wind in the incoherence of the pollen, in the inordinate quantity produced (as in the Coniferæ, Spinage, &c.), in the dangling anthers well fitted to shake out the pollen, in the absence or small size of the perianth or in the protrusion of the stigmas at the period of fertilization, in the flowers being produced before they are hidden by the leaves, in the stigmas being downy or plumose (as in the Gramineæ, Docks, and other plants) so as to secure the chance-blown grains. In plants which are fertilized by the wind, the flowers do not secrete nectar, their pollen is too incoherent to be easily collected by insects, they have not bright-coloured corollas to serve as guides, and they are not, as far as I have seen, visited

by insects. When insects are the agents of fertilization (and this is incomparably the more frequent case both with plants having separated sexes and with hermaphrodites), the wind plays no part, but we see an endless number of adaptations to ensure the safe transport of the pollen by the living workers. We can recognize these adaptations most easily in irregular flowers; but they do not the less occur in perfectly regular flowers, of which those of *Linum* offer an instance, as I will almost immediately endeavour to show.

I have already alluded to the rotation of each separate stigma in the long-styled form alone of *Linum perenne*. In the other species examined by me, and in both forms when the species are dimorphic, the stigmatic surfaces face the centre of the flower, and the furrowed backs of the stigmas, to which the styles are attached, face the circumference. This is the case, in the bud, with the stigmas of the long-styled flowers of *L. perenne*. But by the time the flower in this form has expanded, the five stigmas, by the torsion of that part of the style which lies beneath the stigma, twist round and face the circumference. I should state that the five stigmas do not always perfectly turn round, two or three often facing only obliquely towards the circumference. My observations were made during October; and it is not improbable that earlier in the season the torsion would have been more perfect; for after two or three cold and wet days the movement was very incomplete. The flowers should be examined shortly after their expansion; for their duration is brief, and, as soon as they begin to wither, the styles become spirally twisted together, and the original position of the parts is lost.

He who will compare the structure of the whole flower in both forms of *L. perenne* and *grandiflorum*, and, I may add, of *L. flavum*, will, I think, entertain no doubt about the meaning of this torsion of the styles in the one form alone of *L. perenne*, as well as the meaning of the divergence of the stigmas in the short-styled forms of all three species. It is absolutely necessary, as we now know, that insects should reciprocally carry pollen from the flowers of the one form to those of the other. Insects are attracted by five drops of nectar, secreted exteriorly at the base of the stamens, so that to reach these drops they must insert their proboscides outside the ring of broad filaments, between them and the petals. In the short-styled form of the above three species, the stigmas face the axis of the flower; and had the styles retained their original upright and central position, not only would the stigmas have presented their backs to insects as they sucked the flowers, but they

would have been separated from them by the ring of broad filaments, and could never have been fertilized. As it is, the styles diverge greatly and pass out between the filaments. The stigmas, being short, lie within the tube of the corolla; and their papillous faces, after the divergence of the styles, being turned upwards are necessarily brushed by every entering insect, and thus receive the required pollen.

In the long-styled form of *L. grandiflorum*, the parallel anthers and stigmas, slightly diverging from the axis of the flower, project only a little above the tube of the somewhat concave corolla; and they stand directly over the open space leading to the drops of nectar. Consequently when insects visit the flowers of either form (for the stamens in this species occupy the same position in both forms), they will get their proboscides well dusted with the coherent pollen. As soon as the insect inserts its proboscis to a little depth into the flower of the long-styled form, it will necessarily leave pollen on the faces and margins of the long stigmas; and as soon as the insect inserts its proboscis to a rather greater depth into the short-styled flowers, it will leave pollen on their upturned stigmatic surfaces. Thus the stigmas of both forms will indifferently receive the pollen of both forms; but we know that the pollen alone of the opposite form will produce any effect and cause fertilization.

Long-styled form of *L. perenne*, var. *Austriacum*, with the petals and calyx removed on the near side.

In the case of *L. perenne*, affairs are arranged a little more perfectly; for the stamens in the two forms stand at different heights,

and pollen will adhere to different parts of an insect's body, and will generally be brushed off by the stigmas of corresponding height, to which stigmas each kind of pollen is adapted. In this species, the corolla is flatter, and in the one form the stigmas and in the other form the anthers stand at some height above the mouth of the corolla*. These longer stigmas and longer stamens do not diverge greatly; hence insects, especially rather small ones, will not insert their proboscides between the stigmas or between the anthers, but will strike against them, at nearly right angles, with the backs of their head or thorax. Now, in the long-styled flowers of *L. perenne*, if each stigma had not rotated on its axis, insects in visiting them would have struck their heads against the backs of the stigmas; as it is, they strike against the papillous fronts of the stigmas, and, their heads being already charged with the proper coherent pollen from the stamens of corresponding height borne by the flowers of the other form, fertilization is perfectly effected.

Thus we can understand the meaning of the torsion of the styles in the long-styled flowers alone, as well as their divergence in the short-styled flowers.

One other point is worth a passing notice. In botanical works many flowers are said to be fertilized in the bud. This rests solely, as far as I can discover, on the anthers opening in the bud; no evidence is adduced that the stigma is at this period mature, or that, if then penetrated by pollen-tubes, it is not subsequently, after the expansion of the flower, acted on by pollen brought from other flowers. In the case of *Cephalanthera grandiflora* I have shown† by experiment that insufficient precocious self-fertilization, together with subsequent full fertilization, is the regular course of events. The belief that flowers of any plant are habitually fertilized in the bud, or are perpetually self-fertilized, is a most effectual bar to really understanding their structure. I am far from wishing to say that some flowers, in certain seasons, are not fertilized in the bud: I have reason to believe that some flowers are frequently fertilized without expanding; but my observations lead me to disbelieve that this is ever the invariable

* I neglected to get drawings made from fresh flowers of the two forms. Mr. Fitch has made the above sketch of a long-styled flower from dried specimens and published engravings: his well-known skill ensures accuracy in the proportional size of the parts; and I believe their relative position is true.

† Fertilization of Orchids, p. 108.

course with all the flowers of any species whatever. As it is difficult to prove without troublesome experiments the falsity of the belief of regular fertilization in the bud, I here notice this subject. An estimable and laborious observer*, resting his belief on the usual kind of evidence, states that in *L. Austriacum* (which is dimorphic and is considered by Planchon as a variety of *L. perenne*) the anthers open the evening before the expansion of the flowers, and that the long-styled stigmas are then almost always fertilized. He asks whether this precocious fertilization in the several species of *Linum* and in other plants is not one cause of the short duration of their flowers. Now we know positively that, so far from *Linum perenne* being fertilized by its own pollen in the bud, its own pollen is as powerless on the stigma as so much inorganic dust.

Linum flavum.—To recur to our more immediate subject, in the long-styled form of this species the pistil is nearly twice as long as in the short-styled form; and the stigmas are longer with the papillæ coarser. In the short-styled form the stigmas diverge and pass out between the filaments. The stamens in the two forms differ in height, and, what is singular, the anthers of the longer stamens are shorter; so that in the short-styled form both stigmas and anthers are shorter than in the other form. The pollen of the two forms does not differ. I have not been able to try any experiments on this species; but a careful observer, Mr. W. C. Crocker, intends proving their reciprocal fertility next summer. As this plant is propagated by cuttings, I have generally found that all the plants in the same garden belong to the same form. On inquiry I have never heard of its seeding in this country; but to anyone wishing to raise seedlings, in all probability the path is now open, namely, by carrying pollen from one form to the other.

I have now shown that three species of *Linum* are dimorphic, besides several races of *L. perenne*, esteemed by some botanists to be distinct species, such as *L. montanum*, *L. Sibiricum*, and *L. Austriacum*. According to Vaucher†, *L. Gallicum*, *L. maritimum*, and *L. strictum* are in the same manner dimorphic, as likewise is, according to Planchon‡, *L. salsoloides*. This latter botanist is the only one who seems to have been struck with the importance of the subject; and he acutely asks whether this dimorphism has not some influence on the manner of fertilization. We thus know of

* Études sur la Géograph. Bot., par Prof. H. Lecoq, 1856, tom. v. p. 325.

† Hist. Physiolog. des Plantes d'Europe, 1841, tom. i. p. 401.

‡ Hooker's London Journ. of Botany, 1848, vol. vii. p. 174.

seven dimorphic species of *Linum*; but as this structure has been overlooked in such common garden-flowers as *L. grandiflorum* and *L. flavum*, it is probably of frequent occurrence.

All the species, however, are certainly not thus characterized. I have examined many specimens of *L. catharticum*, and found in all that the stamens and stigmas were of nearly equal height and the same in all the plants. So, again, I looked, near Torquay, at many flowers of the wild *L. usitatissimum* or *angustifolium* (I know not which), and there was no trace of dimorphism. Again, I raised 111 plants from seed sent me from Kew, incorrectly named *L. Austriacum*; the plants were tall and straight, having a rather different aspect from the wild species seen at Torquay, with extremely fugacious blue flowers: in all these plants the stigmas stood on a level with the anthers or projected a very little above them. I protected the flowers from insects; but every one of the 111 plants produced plenty of seed. I mention this fact because it had occurred to me that possibly a species might be dimorphic in function, though not in structure.

Lastly, *Linum Lewisii*, which is ranked by Planchon as a variety of *L. perenne*, but which, now that we know the meaning of reciprocal dimorphism, surely deserves specific honours, must not be passed over. According to Planchon*, the same plant bears some flowers with anthers and stigmas of the same height, and others with styles either longer or shorter than the stamens; so that the same individual plant is trimorphic. This, as far as I know, is a unique case. From analogy we may pretty safely predict the function of the three kinds of flowers: those with stigmas and anthers of the same height will be self-fertile; those with these organs of unequal height will require reciprocal fertilization. A plant of *L. grandiflorum* or of the other dimorphic species, growing by itself, could no more perpetuate its race than could one sex of a diœcious plant, nor could any number of plants without the aid of insects. A single plant of *Linum Lewisii*, on the other hand, in all probability could propagate itself, even if no insects were present, as probably sometimes occurs in its Arctic home. If insects visited the plant, the flowers which were dimorphic would be fertile one with another or with those on any neighbouring plant. Thus the plant would receive the advantage of a cross.

* Hooker's London Journ. of Botany, 1848, vol. vii. p. 175. It is not improbable that the allied genus *Hugonia* is dimorphic; for (p. 525) one species is described "staminibus exsertis;" another has "stamina 5, majora, stylos longe superantia;" and another is furnished "stylis staminibus longioribus."

That this is an advantage, and is one great end gained by reciprocal dimorphism, I can entertain no doubt. That in some cases this dimorphism may be a step towards a complete separation of the sexes, I will not dispute; but good reasons could be assigned to show that there is no necessary connexion between reciprocal dimorphism and a tendency to diœcious structure. Although good is gained by the inevitable crossing of the dimorphic flowers, yet numerous other analogous facts lead me to conclude that some other quite unknown law of nature is here dimly indicated to us.

On the Form of the Vascular Fasciculi in certain British Ferns. By Arthur H. Church, B.A. Oxon. Communicated by W. Francis, Ph.D., F.L.S.

[Read Dec. 18, 1862.]

The distribution of the vascular tissues in the stem and stipes of the British species of Ferns has been made the subject of much interesting and accurate study by Dr. Ogilvie*. His papers are to be found in the 'Annals and Magazine of Natural History' for December 1859 and November 1860. My own long-continued examination of the living plants has not enabled me to detect any but the most trivial mistakes in these full and admirable memoirs. I have therefore only to propose a few slight alterations in Dr. Ogilvie's conclusions, and to make one or two additional remarks on certain species and varieties which he omits to notice. The present communication may be deemed the first instalment of such supplementary observations. I may also here state that I

* The following list of papers includes nearly all those in which the vascular tissues of Ferns have been discussed:—

Presl. Tentamen Pteridographiæ. Pragæ: 1836.

Fée. Die Gefässbündel im Stipes der Farne. Pragæ: 1847.

Ogilvie, Dr. Ann. & Mag. Nat. Hist. 1859 and 1860.

Duval-Jouve, J. Etudes sur le Pétiole des Fougères. In Billot's Archives de la Flore de France; pp. 57 & 149.

King. On Sigillaria. Edinburgh Phil. Trans. 1844.

Leighton, Rev. W. A. Hints on a new character in Ferns. Phyt. n. s. i. p. 256.

Moore, T. The Vascular Bundles of the Stipes of Ferns. Phyt. n. s. i. p. 378.

Reichardt, H. W. Ueber der Gefässbündel Vertheilung im Stamme und Stipes der Farne. Denkschriften der Kaiserlichen Akademie der Wissenschaften, xvii^ter Band. Wien: 1859.

can confirm the general accuracy of Duval-Jouve's figures so far as they relate to species found in Britain.

To discuss the difficult question of the nomenclature of these plants is beside my purpose; I shall therefore do no more than designate each form named by two or three of its best-known synonyms. At the same time, it seems that the results of such inquiries as the present, as possibly affording criteria of generic if not of specific difference, cannot be wholly disregarded, and may ultimately aid us in arriving at a more consistent classification for the Filices.

The genera *Polystichum* and *Lastrea* as understood by Moore and many other authors are respectively coextensive (so far as our native ferns are concerned) with the genera *Aspidium* and *Nephrodium* adopted by Hooker in his 'British Ferns' (1862). I have examined transverse sections of the stipes of all the generally received species and many of the varieties included under these generic appellations, and in two species only did I find any material departure from that one particular arrangement of the vascular fasciculi which is disclosed by a transverse stipital section of such a form as Moore's *Lastrea Filix-mas* or *Polystichum Lonchitis*. In *Nephrodium Filix-mas*, *N. rigidum*, *N. cristatum*, *N. spinulosum* α. *bipinnatum*, β. *dilatatum*, γ. *æmulum*, δ. *dumetorum*, *Aspidium aculeatum* α. *lobatum*, β. *intermedium*, γ. *angulare* of Hooker, and also in the forms *Lophodium glandulosum*, *L. uliginosum*, *L. nanum*, and *L. collinum* of Newman, the same disposition of the vascular tissue occurs. The two notable exceptions to which I have before alluded are found in *Nephrodium Thelypteris* and *N. Oreopteris* of Hooker, identical with the *Lastrea Thelypteris* and *L. montana* of Moore and the *Hemestheum Thelypteris* and *Lastrea* (*Hemestheum*) *montana* of Newman. In fig. 1 the prevalent arrangement is shown; in fig. 2 that which occurs in the mountain fern; while fig. 3 represents that of the marsh fern, which I will now more particularly describe. In all cases the sections noticed are those of the stipes, not of the stem; and I have freely availed myself of the use of a very weak solution of perchloride of iron, in order that the tracts containing tannin might be distinctly marked out.

Nephrodium Thelypteris, Hooker.
Hemestheum Thelypteris, Newman.
Lastrea Thelypteris, Moore.

The present plant is not only closely connected in many of its

integra, glabra, supra lucida; nervi laterales 12–15 utrinque costaque utraque pagina prominuli; petiolus usque pollicem fere longus, teres, glaber. Amenta axillaria, geminata, rarius abortu solitaria, breviter ($\frac{1}{3}$ poll.) pedunculata, subtus nuda, supra floribus masculis densissime obducta, fœmineis paucis multo majoribus intermixtis. Bracteolæ trigono-peltatæ, minutæ, pilosulæ, ciliolatæ, virides. Flores sessiles, compacti, viridiusculi, dein albescentes. Sepala florum masc. basi in tubum brevem connata, extus pilosula, ea flor. fœm. libera, exteriora pubera, dein hirtella, interiora lævia, teneriora. Achænium pisi majoris magnitudine, stylo persistente auctum, perigonio hirtello inclusum, maturescens contactu etiam levi elastice (ad 6 metr.) exsiliens.

In sylvis Sumatræ; in prov. Palembang; in prov. Padang prope Lumut et ad littora prope Siboga, *Teijsmann*. Ins. Singapora, *T. Anderson, M.D.*

Nom. vernac. Kapinie.

Synon. Artocarpus elongatus, *Miq. Fl. Ind. Bat. Suppl.* p. 172 et 419.

TAB. XIII. fig. 1. Ramus floriferus magnit. nat.; fig. 2. Flos ♂ et ♀ auct. ut fig. sequent.; fig. 3. Sepalum exter. fl. ♀ a dorso; fig. 4. Sepal. inter. fl. ♀; fig. 5. Ovarium; fig. 6. idem, verticaliter transsect.; fig. 7. Semen, tegmento remoto.

On the Sexual Relations of the Three Forms of *Lythrum salicaria*. By CHARLES DARWIN, F.R.S., F.L.S., &c.

[Read June 16, 1864.]

SOME of the species of *Lythrum* offer in their manner of fertilization a more remarkable case than can, perhaps, be found in any other plant or animal. In *Lythrum salicaria* three plainly different forms occur: each of these is an hermaphrodite, each is distinct in its female organs from the other two forms, and each is furnished with two sets of stamens or males differing from each other in appearance and function. Altogether there are three females and three sets of males, all as distinct from each other as if they belonged to different species; and if smaller functional differences are considered, there are five distinct sets of males. Two of the three hermaphrodites must coexist, and the pollen be carried by insects reciprocally from one to the other, in order that either of the two should be fully fertile; but unless all three forms coexist, there will be waste of two sets of stamens, and the organization of the species, as a whole, will be imperfect. On the other hand, when all three hermaphrodites coexist, and the pollen is carried from one to the other, the scheme is perfect; there is no waste of pollen and no false co-adaptation. In short, nature has ordained a most complex marriage-arrangement, namely a triple union between three hermaprodites,—each her-

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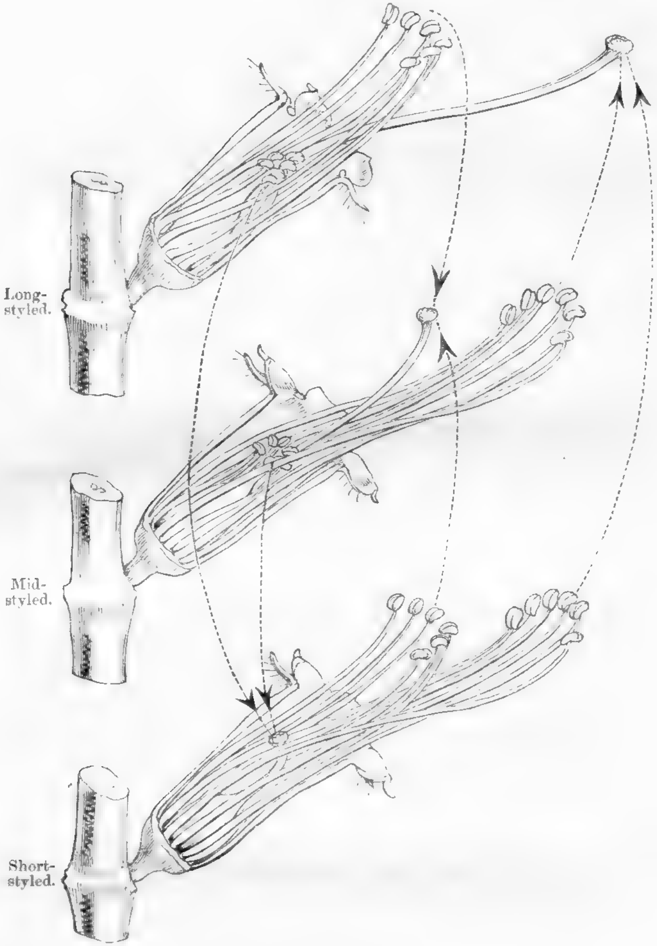
Mo. Bot. Garden,

maphrodite being in its female organ quite distinct from the other two hermaphrodites and partially distinct in its male organs, and each furnished with two sets of males.

The three forms may be conveniently called, from the unequal lengths of their pistils, the *long-styled*, *mid-styled*, and *short-styled*. Their existence and differences were first observed by Vaucher*, and subsequently more carefully by Wirtgen; but, not being guided by any theory, neither author perceived some of the most curious points of difference. I will first briefly describe the three forms by the aid of the accompanying accurate diagram, which shows the flowers, six times magnified, in their natural position, with their petals and the near side of the calyx removed.

Long-styled form.—This can at once be recognized by the length of the pistil, which is (including the ovarium) fully one-third longer than that of the mid-styled, and more than thrice as long as that of the short-styled form. It is so disproportionately long, compared with the flower, that it projects in the bud through the unfolded petals. It stands out considerably beyond the longer stamens; its terminal portion depends a little, but the stigma itself is slightly upturned: the globular stigma is considerably larger than that of the other two forms. The six longer stamens project about two-thirds of the length of the pistil, and correspond in length with the pistil of the mid-styled form. The correspondence with the pistil in length in this and the two following cases is generally very close; the difference, where there is any, being usually in a slight excess of length in the stamens. The six shorter stamens (each of which alternates with a longer one) lie concealed within the calyx; their ends are upturned, and they are graduated in length, so as to form a triple row—both which characters are here much more marked than with the longer stamens, which vary in these respects. The anthers of the shorter stamens are smaller than those of the longer stamens. Knowing that the pollen differs greatly in the longer and shorter stamens of the two other forms, I carefully compared that of the two sets of stamens in this form: in both the pollen-grains are yellow, but they are a little larger in the longer than in the shorter stamens. The difference is slight, so that I convinced myself of its reality only by putting two small heaps close together under the compound mi-

* Hist. Phys. des Plantes d'Europe, tom. ii., 1841, p. 371. Wirtgen, "Ueber *Lythrum salicaria* und dessen Formen," Verhand. des naturhist. Vereins der preuss. Rheinl., 5. Jahrgang, 1848, S. 7.



Diagrams of the flowers of the three forms of *Lythrum salicaria*, in their natural position, with the petals removed and with the near side of the calyx cut away: enlarged six times.

The dotted lines with the arrows show which pollen must be applied to each stigma to cause full fertility.

croscope, and I found I could always (with one exception) distinguish them: I then showed the specimens to two other persons, and they likewise distinguished the two kinds and pointed out which was the largest. The capsules of this form contain, on an average, 93 seeds: how this average was obtained will presently be explained. I repeatedly observed that the seed, when cleaned, seemed larger than that from the mid-styled or short-styled forms; consequently I placed 100 long-styled seeds in a good balance, and by the double method of weighing found that they equalled 121 seeds of the mid-styled and 142 of the short-styled; or, in short, that five long-styled seeds equalled six mid-styled and seven short-styled seeds. These slight differences in the weight of the seed, and, as we shall soon see, in the average number produced, are worth recording, as they characterize not mere varieties but coexisting forms of the same species.

Mid-styled form.—The pistil occupies the position represented in the diagram, with its extremity considerably, but in a variable degree, upturned; the stigma is seated between the anthers of the long and the short stamens. The six longer stamens correspond in length with the pistil of the long-styled form; their filaments are coloured bright pink; the anthers are dark-coloured, but from containing bright green pollen and from their early dehiscence they appear emerald-green. Hence the general appearance of these stamens is remarkably dissimilar from that of the longer stamens of the long-styled form. The six shorter stamens, enclosed within the calyx, resemble in all respects the shorter stamens of the long-styled form, and both correspond in length with the short pistil of the short-styled form. The green pollen-grains of the longer stamens are plainly larger than the yellow pollen-grains of the shorter anthers: this fact was conspicuous in several camera-lucida drawings made for me by my son, Mr. W. E. Darwin. There is some variability in size, but $\frac{12}{7000}$ of an inch may be taken as about the average diameter of the green pollen-grains when distended with water, and $\frac{9}{7000}$ as the diameter of the yellow grains of the shorter stamens; so that the difference in diameter is in about the proportion of four to three. The capsules contain, on an average, 132 seeds; but, perhaps, as we shall see, this is rather too high an average. The seeds themselves are smaller than those of the long-styled form.

Short-styled form.—The pistil is here very short, not one-third of the length of that of the long-styled form. It is enclosed within the calyx, which, differently from in the other two forms,

does not enclose any anthers. The end of the pistil is generally bent upwards at right angles. The six longer stamens, with their pink filaments and green pollen, resemble in size of the grains and in all respects the longer stamens of the mid-styled form, and both correspond in length with the long-styled pistil. The six shorter stamens, with their uncoloured filaments and yellow pollen, resemble in size of the grains and in all respects the longer stamens of the long-styled form, and both correspond in length with the mid-styled pistil. The capsules contain fewer seeds on an average than in either of the preceding forms, namely 83·5, and they are considerably smaller in size. In this latter respect, but not in number, there is a gradation parallel to that of the length of the pistil, the long-styled having the largest, the mid-styled the next in size, and the short-styled the smallest seed.

From this description we see that there are three distinct female organs, or rather females as they are borne on distinct individuals, differing in the length and curvature of the style, in the size of the stigma, and in the number and size of the seed. In the three forms, taken together, there are thirty-six stamens or males, and these can be divided into three sets of a dozen each, differing from each other in length, curvature, and colour of the filaments, in the size of the anthers, and especially in the colour and diameter of the pollen-grains. Each of the three forms bears half-a-dozen of one kind of stamens and half-a-dozen of another kind, but not all three kinds. The three kinds correspond in length with the three pistils: the correspondence is always between half the stamens borne by two forms with the pistil of a third form. These remarks apply to the structure, and not, as yet, to the functions, of the reproductive organs.

I ascertained the average number of seed by counting them in eight fine selected capsules taken from plants of the three forms growing wild, and the result was, as we have seen, for the long-styled (neglecting decimals) 93, mid-styled 132, and short-styled 83. I should not have trusted this result, but I had a number of plants in my garden which, from their youth, did not yield the full complement of seed, but they were of exactly the same age and grew under exactly the same conditions, and were freely visited by bees. I took six fine capsules from each, and found the average to be for the long-styled 80, for the mid-styled 97, and for the short-styled 61. Lastly, I made numerous artificial unions, and, as may be seen in the following Tables, these gave in the long-styled an average of 90 seeds, in the mid-styled 117,

and in the short-styled 71. So that we have good concurrent evidence of the different average production of seed by the three forms. To show that the artificial fertilizations, presently to be described, produced their full effect and may be trusted, I may state that one mid-styled capsule yielded 151 good seeds, which is the exact number of the finest wild capsule examined by me. Artificially fertilized short- and long-styled capsules actually produced a greater number of seeds than I have found in wild plants, but then I did not examine many of the latter. This Lythrum, I may add, offers a remarkable instance, how profoundly ignorant we are of the life-conditions of each species: naturally it grows "in wet ditches, watery places, and especially on the banks of streams," and though it produces so many minute seeds, it never spreads on the adjoining land; yet, planted in my garden, on clayey soil lying over the chalk, and which is so dry that a rush cannot be found, it thrives luxuriantly, grows to above six feet in height, produces self-sown seedlings, and (which is a severer test) is fully as fertile as in a state of nature. Nevertheless it would be almost a miracle to find this plant spontaneously growing on such land as my garden, though under its native climate.

According to Vaucher and Wirtgen, the three forms coexist in all parts of Europe. Some friends gathered for me in North Wales a number of twigs from separate plants growing near each other, and then classified them. My son did the same in Hampshire, and here is the result:—

	Long-styled.	Mid-styled.	Short-styled.	Total.
North Wales	95	97	72	264
Hampshire.	53	38	38	129
Total....	148	135	110	393

If twice or thrice the number had been collected, probably the three forms would have been found nearly equal; I infer this from considering the above figures, and from my son telling me that if he had collected in another spot, he felt sure that the mid-styled plants would have been in excess. I several times sowed small parcels of seed, and raised all three forms; but I neglected to record the parent form, except in one instance, in which I raised from short-styled seed twelve plants, of which only one turned out long-styled, four mid-styled, and seven short-styled.

Insects are necessary for the fertilization of this Lythrum. During two years I kept two plants of each form protected, and in the autumn they presented a remarkable contrast in appearance with the adjoining uncovered plants, which were densely covered with capsules. In 1863 a protected long-styled plant produced only five poor capsules; two mid-styled plants produced the same number; and two short-styled plants between them produced only one: these capsules contained very few seed; yet the plants were fully productive when artificially fertilized under the net. In a state of nature the flowers are incessantly visited for their nectar by hive- and humble-bees and various Diptera. The nectar is secreted all round the base of the ovarium; but a passage is formed along the upper and inner side of the calyx by the lateral deflection (not represented in the diagram) of the basal portions of the filaments; so that insects invariably alight on the upper side of the flowers, on the projecting stamens and pistil, and insert their probosces along the upper inner margin of the calyx. We can now see why the ends of the stamens with their anthers, and the ends of the pistils with their stigma, are a little upturned, in order that they may brush against the lower hairy surfaces of the insects' bodies. The short stamens which lie enclosed within the calyx of the long- and mid-styled forms can be touched only by the proboscis and the narrow chin of the sucking bee; hence they have their ends more upturned, and they are graduated in length, so as to fall into a narrow file, three deep, sure to be raked by the thin intruding proboscis. The anthers of the longer stamens stand laterally further apart and are more nearly of the same length, for they have to brush against the whole breadth of the insect's body. I may here incidentally remark, that in very many flowers the pistil, or the stamens, or both, are rectangularly bent to one side of the flower: this bending may be permanent, as with *Lythrum* and many others, or may be effected (as in *Dictamnus fraxinella* and many others) by a temporary movement which occurs in the stamens when the anthers dehisce, and in the pistil when the stigma is mature; but these two movements are by no means always contemporaneous in the same flower. Now I have found no exception to the rule, that when the stamens and pistil are bent, the bending is exactly to that side of the flower which secretes nectar (even though there be a rudimentary nectary of large size on the opposite side, as in some species of *Corydalis*); or, when nectar is secreted on all

sides, to that side where the structure of the flowers allows the easiest access to it, as in *Lythrum*, Papilionaceous flowers, and many others. The rule consequently is that when the pistil and stamens are bent, the stigma and anthers are brought into the pathway towards the nectary. There are a few cases which seem to be exceptions, but they are not so in truth: for instance, in the Gloriosa lily, the stigma of the grotesque and rectangularly bent pistil is brought, not into the pathway from the open air towards the nectar-secreting recesses of the flower, but into the circular route from one nectary to the other; in *Scrophularia aquatica* the pistil is bent downwards from the mouth of the flower, but it thus strikes the pollen-dusted breasts of the wasps which habitually visit these ill-scented blooms. In the above rule we see one more instance of the supreme dominating power of insects over all the minor structural details of flowers, especially of those which have irregular corollas. Flowers which are fertilized by the wind must of course be excepted, but I do not know of a single instance of an irregular flower which is fertilized or crossed by this means.

I have delayed too long on these points, but I must allude to one other. We have seen that the three pistils of different lengths have each two half-dozen sets of stamens of corresponding length. When bees suck the flowers, the longest stamens, bearing the green pollen, rub against the abdomen and the interior sides of the posterior legs, as does likewise the stigma of the long-styled form. The stamens of middle length and the stigma of the mid-styled form rub against the under side of the thorax and between the front pair of legs. The shortest stamens and the stigma of the short-styled form must rub against the proboscis and chin; for the bees in sucking insert only the front of their heads into the calyx. On catching bees, I observed much green pollen on the inner sides of the hind legs and on the abdomen, and much yellow pollen on the under side of the thorax. There was also pollen on the chin, and, it may be presumed, on the proboscis, but this was difficult to observe. I had, however, independent proof that pollen is carried on the proboscis; for in a protected short-styled plant (which produced only two capsules) one small branch was accidentally left during many days pressing against the fine net, and bees were seen inserting their probosces through the meshes, and in consequence numerous capsules were formed on this one small branch. From these several facts it follows that insects would chiefly carry to the

stigma of each form pollen from the stamens of corresponding length; and we shall presently see the importance of this adaptation. It must not, however, be supposed that the bees do not get more or less dusted all over with the several kinds of pollen; they certainly do, as could be seen with the green pollen from the longest stamens. Moreover, a case will presently be given of a long-styled plant which grew absolutely by itself, and produced an abundance of capsules, which must have been fertilized by its own two kinds of pollen; but these capsules contained a very poor average of seed. Hence insects, and chiefly bees, act both as general carriers of pollen, and as special carriers of the right kind *.

Variability.—Before passing on to more important topics, I must say a few words on this head. Wirtgen remarks † on the variability in the branching of the stem, in the length of the bracteæ, size of the petals, and in several other respects. The plants now growing in my garden have their leaves arranged oppositely, alternately, and in whorls of three, and differ greatly in shape. The stems of the plants bearing leaves in whorls are hexagonal; those of the other plants are quadrangular. But we are concerned only with the reproductive organs: the upward bending of the pistil is variable, and in a remarkable degree in the short-styled form, in which it is sometimes straight, sometimes slightly curved, but generally upturned at right angles. The stigma of the long-styled pistil frequently has longer papillæ or is rougher than that of the mid-styled, and this than that of the short-styled form; but this character, though fixed and uniform with the two forms of *Primula*, is here variable, and I have

* In my paper on the two forms of *Primula* (Journal Proc. Linn. Soc. 1862, p. 85) I stated that I had only occasionally seen humble-bes sucking the flowers of the Cowslip (*P. veris*). Since then I have had some beds in my garden containing nearly 700 plants, and these were incessantly visited by *Bombus hortorum* and *B. muscorum*. I caught some of these bees, and I found (as I had anticipated in my paper, p. 86) that a vast majority of the pollen-grains which adhered to the base of the proboscis were large-sized and had come from the long stamens of the short-styled form, and were thus placed ready to fertilize the stigma of the long-styled form. On the other hand, on the middle, and near the tip of the proboscis, a very large proportion of the pollen-grains were of the small size, and had come from the short stamens of the long-styled form. My son caught, also, a moth (*Cucullia verbasci*) hovering over the bed, and I found on its proboscis a similar distribution of the two kinds of pollen-grains. I give these facts as a further illustration of the importance of the relative lengths of the stamens and pistil.

† Verhand. des naturhist. Vereins, 5. Jahrgang, 1848, S. 11, 13.

seen mid-styled stigmas rougher than those of the long-styled. The degree to which the longer and middle stamens are graduated in length and are upturned at their ends is variable; sometimes all are equal. The colour of the green pollen in the long stamens is variable *, and is sometimes pale greenish yellow; in one short-styled plant it was almost white. The grains vary a little in size: I examined one short-styled plant with the grains above the average size; and I have seen a long-styled plant with undistinguishable grains from the longer and shorter anthers. We have here considerable fluctuations of character; and if any of these slight structural differences were of direct service to the plant, or were correlated with useful functional differences, we can perceive that the species is just in that state in which natural selection might readily do much for its modification.

To return to our proper subject—we see that there are three kinds of females and three kinds of males, each kind of the latter being borne by half-dozens on two of the three forms. It remains to discover whether these several sexes or sexual organs differ from each other in function. Nothing brings more prominently forward the complexity of the reproductive system of this extraordinary plant, than the necessity, in order to ascertain the above fact, of artificially making eighteen distinct unions. Thus the long-styled form had to be fertilized with pollen from its own two distinct kinds of anthers, from the two in the mid-styled, and from the two in the short-styled form. The same process had to be repeated with both the mid- and short-styled forms. It might have been thought sufficient to have tried on each stigma the green pollen, for instance, from either the mid- or short-styled longer stamens, and not from both; but the result proves that this would have been insufficient, and that it was necessary to try all six kinds of pollen on each stigma. As in artificial fertilizations there will always be some failures, it would have been advisable to have

* *Lagerstrœmia Indica*, one of the Lythraceæ, is strangely variable in its stamens—I presume in part due to its growth in a hothouse. The most perfect flowers produced with me five very long stamens with thick flesh-coloured filaments and green pollen, and from nineteen to twenty-nine short stamens with yellow pollen; but many flowers produced only one, two, three, or four long stamens with green pollen, which in some of the anthers was wholly replaced by yellow pollen; one anther offered the singular case of half, or one cell being filled with bright green, and the other cell with bright yellow pollen. One petal had a furrow near its base, which contained pollen. According to analogy with *Lythrum*, this species would produce three forms; if so, the above plant was a mid-styled form: it was quite sterile with its own two kinds of pollen.

repeated each of the eighteen unions a score of times; but the labour would have been too great; as it was, I made 223 artificial unions; *i. e.*, I fertilized, on an average, above a dozen flowers in the eighteen different methods. Each flower was castrated; the adjoining buds had to be removed, that the marking-thread, wool, &c. might be safely secured; and after each fertilization the stigma had to be examined with a lens to see that there was sufficient pollen. Plants of all three forms were protected during two years by large nets on a framework; two plants were used during one or both years, in order to avoid any individual peculiarity in any one plant. As soon as the flowers withered, the nets were removed; and in the autumn the capsules were daily inspected; when the seeds were ripe they were counted under the microscope. I have given these details that confidence may be placed in the following Tables, and as some excuse for two blunders which, I believe, I made. These blunders are referred to, with their probable causes, in two notes to the Tables; the erroneous numbers, however, are entered in the Tables, that it may not be supposed that I have in any one instance tampered with the results.

A few words explanatory of the three Tables must be given. Each is devoted to one form, and is divided into six compartments. The two upper ones in each table give the product of good seed from the application of pollen from the two sets of stamens which correspond in length with the pistil of that form. The two next lower compartments show the result of pollen from the other two sets of stamens, which do not correspond in length with the pistil, and which are borne by the same two forms. The two lowest compartments show the result of the application of each form's own two kinds of pollen. The term "own pollen," used here and in the Tables, does not mean pollen from the flower to be fertilized —for this was never used—but from another flower on the same plant, or more commonly from a distinct plant of the same form. In the result given, "0" generally means that no capsule was produced, or that the capsule contained no good seed. In some part of each row of figures in each compartment, a short horizontal line may be seen; the unions above this line were made in 1862, and below it in 1863. It is of importance to observe this, as it shows that the same general result ensued in two successive years; but more especially because 1863 was a very hot and dry season, and the plants had occasionally to be watered. This did not prevent the full complement of seed being produced from

the more fertile unions; but it rendered the less fertile unions even more sterile than they otherwise would have been. I have seen striking instances of this same fact in making homomorphic and heteromorphic unions in *Primula* *; and it is well known that the conditions of life must be highly favourable to give any chance of producing hybrids from species which cross with difficulty.

Table I.—Long-styled Form.

I.		II.	
13 flowers fertilized by the longer stamens of the mid-styled. *These stamens equal in length the pistil of the long-styled.*		13 flowers fertilized by the longer stamens of the short-styled. *These stamens equal in length the pistil of the long-styled.*	
Product of good seed in each capsule.		Product of good seed in each capsule.	
36	53	159	104
81	0	43	119
0	0	96 poor seed.	96
0	0	103	99
0	0	0	131
—	0	0	116
45		—	
41		114	
38 per cent. of these flowers yielded capsules. Each capsule contained, on an average, 51·2 seed.		84 per cent. of these flowers yielded capsules. Each capsule contained, on an average, 107·3 seed.	

* In the spring of 1862 I crossed forty Cowslip flowers (*P. veris*) heteromorphically and homomorphically. The plants were accidentally exposed in the greenhouse to too hot a sun, and a number of umbels perished. Some, however, remained in moderately good health, and on these there were twelve flowers which had been fertilized heteromorphically and eleven which had been fertilized homomorphically. The twelve heteromorphic unions yielded seven fine capsules, containing on an average 57·3 good seed. Now mark the difference: the eleven homomorphic unions yielded only two capsules, of which one contained 39 seeds, but so poor, that I do not suppose one would have germinated, and the other only 17 fairly good seed. It would be superfluous to give any more details on this experiment, or on some which I made at the same time on *P. Sinensis*, after the appearance of Mr. John Scott's admirable paper on the various dimorphic species of *Primula*, in which he confirms my former results, and adds many original and valuable observations. Dr. Hildebrand has also (Botanische Zeitung, 1864, Jan. 1, S. 3) confirmed my general results with respect to *P. Sinensis*, and has corrected an error into which in some unaccountable manner I fell, namely, that the pollen-grains from the long- and short-styled forms were of the same size. Dr. Hildebrand has added a series of new and important experiments, for he fertilized homomorphically a number of flowers with pollen from the same form, and likewise from the same individual flower. These latter he found were thus rendered rather more sterile. This experiment, I believe, has never been systematically tried before.

Table I.—Long-styled Form (*continued*).

III.

14 flowers fertilized by the short stamens of the mid-styled.

3	0
0	0
0	0
0	0
0	0
—	0
0	0
0	

Too sterile for any average.

IV.

12 flowers fertilized by the shorter stamens of the short-styled.

20	0
0	0
0	0
0	0
—	0
0	0
0	

Too sterile for any average.

V.

15 flowers fertilized by *own* longer stamens.

2	—
10	0
23	0
0	0
0	0
0	0
0	0
0	0

Too sterile for any average.

VI.

15 flowers fertilized by *own* shorter stamens.

4	—
8	0
4	0
0	0
0	0
0	0
0	0
0	0

Too sterile for any average.

I fertilized a considerable number of flowers with pollen, taken by a camel's-hair brush, from both the long and short stamens of their own (long-styled) form; but I did not examine with a lens (as I did in the cases in the Tables) whether sufficient pollen had been placed on the stigma: only 5 capsules were produced, and these yielded on an average 14·5 seed. In 1863 I tried a much better experiment: a long-styled plant was grown by itself, miles away from any other plant, so that its stigmas could have received only the two kinds of pollen proper to this form. The flowers were incessantly visited by bees, so that the stigmas must have received on the most favourable days, and at the most favourable hours, successive applications of pollen: all who have crossed plants know that this highly favours fertilization. This plant produced an abundant crop of capsules; I took by chance 20, and these (excluding one poor one) contained seed as below:—

20	20	35	21	19
26	24	12	23	10
7	30	27	29	13
20	12	29	19	35

This gives an average of 21·5 seed per capsule; and as we know that this form, when standing near plants of the other two forms and fertilized by insects, produces an average of 93·1 seed per capsule, we see that the long-styled form fertilized by its own two pollens yields only between one-fourth and one-fifth of the full number of seed. I have spoken as if this plant had received both its own kinds of pollen, and this is, of course, possible; but, from the enclosed position of the shorter stamens, it is much more probable that the stigma received almost exclusively the pollen from its own longer stamens.

Table II.—Mid-styled Form.

I.

12 flowers fertilized by the longer stamens of the long-styled. *These stamens equal in length the pistil of the mid-styled.*

Product of good seed in each capsule.

138	122
149	50
147	151
109	119
133	138
144	0
—	

92 per cent. of the flowers (probably 100 per cent.) yielded capsules. Each capsule contained, on an average, 127·3 seed.

II.

12 flowers fertilized by the shorter stamens of the short-styled. *These stamens equal in length the pistil of the mid-styled.*

Product of good seed in each capsule.

112	109
130	143
143	124
100	145
33	12
—	141
104	

100 per cent. of the flowers yielded capsules. Each capsule contained, on an average, 108·0 seed; or, excluding capsules with less than 20 seed, the average is 116·7 seed.

III.

13 flowers fertilized by the short stamens of the long-styled.

83	12	
0	19	seed small and poor.
0	85	seed small and poor.
—	0	
44	0	
44	0	
45	0	

54 per cent. of the flowers yielded capsules. Each capsule contained, on an average, 47·4 seed; or, excluding capsules with less than 20 seed, the average is 60·2 seed.

IV.

15 flowers fertilized by the longer stamens of the short-styled.

130	86
115	113
14	29
6	17
2	113
9	79
—	128
132	0

93 per cent. of the flowers yielded capsules. Each capsule contained, on an average, 69·5 seed; or, excluding capsules with less than 20 seed, the average is 102·8.

V.

12 flowers fertilized by *own* longer stamens.

92	0
9	0
63	0
—	0
136?*	0
0	0
0	

Excluding the capsule with 136 seed, 25 per cent. of the flowers yielded capsules, and each capsule contained, on an average, 54·6 seed; or, excluding capsules with less than 20 seed, the average is 77·5.

VI.

12 flowers fertilized by *own* shorter stamens.

0	0
0	0
0	0
—	0
0	0
0	0
0	

0 per cent. of the flowers yielded capsules.

* I have hardly any doubt that this result of 136 seed is due to a gross error. The flowers to be fertilized by their own longer stamens were first marked by

I fertilized a considerable number of flowers with pollen, taken by a camel's-hair brush, from both the long and short stamens of their own (short-styled) form; but I did not examine with a lens (as I did in the cases in the Tables) whether sufficient pollen had been placed on the stigma: only 5 capsules were produced, and these yielded, on an average, 11·0 seed.

Table III.—Short-styled Form.

I. 12 flowers fertilized by the shorter stamens of the long-styled. *These stamens equal in length the pistil of the short-styled.*		II. 13 flowers fertilized by the shorter stamens of the mid-styled. *These stamens equal in length the pistil of the short-styled.*	
69	56	93	69
61	88	77	69
88	112	48	53
66	111	43	9
0	62	0	0
0	100	0	0
—		—	0
83 per cent. of the flowers yielded capsules. Each capsule contained, on an average, 81·3 seed.		61 per cent. of the flowers yielded capsules. Each capsule contained, on an average, 64·6 seed.	

III. 10 flowers fertilized by the longer stamens of the long-styled.		IV. 10 flowers fertilized by the longer stamens of the mid-styled.	
0	14	0	0
0	0	0	0
0	0	0	0
0	0	0	0
—	0	—	0
23		0	
Too sterile for any average.		Too sterile for any average.	

"white thread," and those by the longer stamens of the long-styled form by "white silk;" a flower fertilized in the latter manner would have yielded about 136 seed, and it may be observed that one such pod is missing, viz., at the bottom of compartment 1. Therefore I have hardly any doubt that I fertilized a flower marked with "white thread," as if it had been marked with "white silk." With respect to the capsule which yielded 92 seed, in the same column with that which yielded 136, I do not know what to think. I endeavoured to prevent pollen dropping from an upper to any lower flower, and I tried to remember to wipe the pincers carefully after each fertilization; but in making eighteen different crosses, sometimes on windy days, and pestered by bees and flies buzzing about, some few errors could hardly be avoided. One day I had to keep a third man by me all the time to prevent the bees visiting the uncovered plants, for in a few seconds' time they might have done irreparable mischief. It was also extremely difficult to exclude minute Diptera from the net. In 1862 I made the great mistake of placing a mid-styled and long-styled under the same huge net: in 1863 I avoided this error.

Table III.—Short-styled Form (*continued*).

V. 10 flowers fertilized by *own* longer stamens.		VI. 10 flowers fertilized by *own* shorter stamens.	
0	0	64?*	0
0	0	0	0
0	0	0	0
—	0	—	0
0	0	21	0
0		9	
Too sterile for any average.		Too sterile for any average.	

I fertilized a number of flowers without particular care with their own two pollens, but they did not produce a single capsule; the position of the stigma within the calyx renders the fertilization without some care difficult.

Summary of the three preceding Tables.

Long-styled form.—Twenty-six flowers fertilized by the stamens of corresponding length, borne by the mid- and short-styled forms, yielded 61·5 per cent. of capsules, which contained, on an average, 89·7 seed.

Twenty-six flowers fertilized by the other and shorter stamens of the mid- and short-styled forms yielded only two very poor capsules.

Thirty flowers fertilized by this form's own two sets of stamens yielded only eight very poor capsules; but flowers well fertilized by bees by one or both of their own kinds of pollen produced numerous capsules containing, on an average, 21·5 seed.

Short-styled form.—Twenty-five flowers fertilized by the stamens of corresponding length, borne by the long- and mid-styled forms, yielded 72 per cent. of capsules, which (excluding one capsule with only nine seeds) contained, on an average, 70·8 seed.

Twenty flowers fertilized by the longer stamens of the long- and mid-styled forms yielded only two very poor capsules.

Twenty flowers fertilized by both their own two sets of stamens yielded only two poor (or perhaps three) capsules.

Mid-styled form.—Twenty-four flowers fertilized by the stamens of corresponding length, borne by the long- and short-styled forms, yielded 96 (probably 100) per cent. of capsules, which con-

* I suspect that, by mistake, I fertilized this flower with the pollen of the shorter stamens of the long-styled form, and it would then have yielded about 64 seed. Flowers to be thus fertilized were marked with black silk; those with the pollen of the shorter stamens of the short-styled with black thread; and thus, I suspect, the mistake arose.

tained (excluding one capsule with 12 seed), on an average, 117·2 seed.

Fifteen flowers fertilized by the longer stamens of the short-styled form yielded 93 per cent. of capsules, which (excluding four capsules with less than 20 seed) contained, on an average, 102·8 seed.

Thirteen flowers fertilized by the shorter stamens of the long-styled form yielded 54 per cent. of capsules, which capsules (excluding one with 19 seed) contained, on an average, 60·2 seed.

Twelve flowers fertilized by own longer stamens yielded 25 per cent. of capsules, which (excluding one with 9 seed) contained, on an average, 77·5 seed.

Twelve flowers fertilized by own shorter stamens yielded not a single capsule.

Considering the three Tables and this summary, we may safely draw the following conclusions. First, that, as in structure so in function, there are three females or female organs: this is manifest; for when all three receive the very same pollen, they are acted on most differently. So conversely with the thirty-six stamens, we know that they consist of three separate sets of a dozen each, differing in various respects; and in function the pollen of these three sets when applied to one and the same stigma acts most differently, as a glance at the Tables proves. But we shall presently see that the action of the pollen of the whole dozen longest and of the whole dozen shortest stamens is not identical. Secondly, we see that only the longest stamens fully fertilize the longest pistil, the middle stamens the middle pistil, and the shortest stamens the shortest pistil. And now we can comprehend the meaning of the almost exact correspondence in length between the pistil of each form and the two half-dozen sets of stamens borne by the two other forms; for the stigma of each form is thus rubbed against the same spot of the insect's body, which becomes most charged with the proper pollen. In all three forms, the female organ is but feebly, or not at all, acted on by its own two kinds of pollen. In my papers on the dimorphism of *Primula* and *Linum*, I used the terms "heteromorphic" for the fully fertile unions between the female element of the one form and the male element of the other, and "homomorphic" for the less fertile or quite sterile unions between the female and male elements of the same form. The principle involved in these terms holds good with *Lythrum*, but is insufficient; for though in each of the three forms the fertile unions are all *heteromorphic*, the ap-

propriate pollen coming from the stamens of corresponding length borne by the other two forms, and though the *homomorphic* unions of the females with their own two sets of males are always more or less sterile, there remain in each case two other sterile unions, not included in these two terms. Hence it will be found convenient to designate the two unions of each female with the two sets of stamens of corresponding length, which are fully fertile, as *legitimate unions*, and the four other, more or less sterile, unions of each female with the four other sets of stamens as *illegitimate unions*. Consequently, of the eighteen possible unions between the three forms, six are legitimate and twelve are illegitimate.

Another and curious conclusion cannot be considered as proved, but is rendered highly probable, by the Tables. The unions of the pistils and stamens of equal length are alone fully fertile. Now with the several illegitimate unions it will be found that the greater the inequality in length between the pistil and stamens, the greater the sterility of the result. There is no exception to this rule. Thus, with the long-styled form, its own shorter stamens are far less equal in length to the pistil than its own longer stamens; and the capsules fertilized by the pollen of the shorter stamens yielded fewer seeds: the same comparative result follows from the use of the pollen of the shorter stamens of the mid-styled form, which are much shorter than the shorter stamens of the short-styled (see diagram), and therefore less equal in length to the long-styled pistil. We shall see exactly the same result if we look to the four illegitimate unions under the mid- and short-styled forms. Certainly the difference in sterility in these several cases is very slight, but the sterility always increases with the increasing inequality of length between the pistil and the stamens which are used. Therefore I believe in the above rule; but a vast number of artificial unions would be requisite to prove it. If the rule be true, we must look at it as an incidental and useless result of the gradational changes through which this species has passed in arriving at its present condition. On the other hand, the correspondence in length between the pistil of each form and those stamens which alone give full fertility is clearly of service to the species, and is probably the result of direct adaptation.

Some of the illegitimate unions yielded, as may be seen in the Tables, during neither year a single seed; but, judging from the case of the long-styled plant, it is probable, if such unions could be effected repeatedly under the most favourable conditions, some few seeds would be produced. Anyhow, I can state that in all

the eighteen possible unions the pollen-tubes penetrated, after eighteen hours, the stigma. I have reason to believe that the offspring from the illegitimate unions present some singular characteristics; but until my observations on this head are repeated, I must be silent. At first I thought that perhaps two kinds of pollen placed together on the same stigma would give more fertility than any one kind; but we have seen that this is not the case with each form's own two kinds of pollen; nor is it probable in any case, as I occasionally got, by the use of single kinds of pollen, fully as many seed as I have seen in a capsule naturally fertilized. Moreover the proper pollen from a single anther is more than sufficient to fully fertilize each stigma; hence, in this as in so many other cases, at least twelve times as much of each kind of pollen is produced as is necessary to ensure full fertilization. From the dusted condition of the whole body of those bees which I caught on these flowers, it is probable that some pollen of all kinds is deposited on each stigma; but there can hardly be a doubt that the pollen of the stamens of corresponding length will be prepotent and will wholly obliterate any effect from the other kinds of pollen, even if previously deposited on the stigma. I infer this partly from the fact ascertained by Gärtner that each species' own pollen is so prepotent over that of any other species, that if put on the stigma many hours subsequently, it will entirely obliterate the action of the foreign pollen. But I draw the above inference especially from the following experiment: I fertilized homomorphically or illegitimately some long-styled Cowslip flowers (*Primula veris*) with their own pollen, and exactly twenty-four hours subsequently I fertilized these same stigmas heteromorphically or legitimately with pollen from a short-styled dark-red Polyanthus. I must premise that I have raised many seedlings from crossed Cowslips and Polyanthus, and know their peculiar appearance; and I further know, by the test of the fertility of the mongrels *inter se*, and with both parent forms, that the Polyanthus is a variety of the Cowslip, and not of the Primrose (*P. vulgaris*) as some authors have supposed. Now from the long-styled Cowslip twice fertilized in the manner explained, I raised twenty-nine seedlings, and every one of them had flowers coloured more or less red; so that the heteromorphic Polyanthus-pollen wholly obliterated the influence of the homomorphic pure Cowslip-pollen, which had been placed on the stigmas twenty-four hours previously, and not a single pure Cowslip was produced.

The last conclusion which may be deduced from the Tables, even from a glance at them, is that the mid-styled form differs from both the others in its much higher capacity for fertilization. Not only did the twenty-four flowers fertilized by the stamens of corresponding lengths, all, or all but one, yield capsules rich in seed; but of the other four illegitimate unions, that by the longer stamens of the short-styled form was highly fertile, though less than in the two legitimate unions, and that by the short stamens of the long-styled form was fertile to a considerable degree; the two unions with this form's own pollen were sterile, but in different degrees. So that the mid-styled form, when fertilized by the six kinds of pollen, evinces five different grades of fertility. By comparing compartments 3 and 6 in Table II. we learn a remarkable fact, namely, that though the pollen from the short stamens of the long-styled and from this form's own (mid-styled) short stamens, used in these two unions, is identical in all respects, yet that its action is widely different; in the one case above half the fertilized flowers yielded capsules containing a fair number of seed; in the other case not one single capsule was produced. So, again, the green, large-grained pollen from the long stamens of the short-styled and from this form's own (mid-styled) long stamens is identical in all respects, but its action, as may be seen in compartments 4 and 5, is widely different. In both these cases the difference in action is so plain that it cannot be mistaken, but it can be corroborated. If we look to Table III., to the legitimate action of the short stamens of the long- and mid-styled forms on the pistil of the short-styled form, we again see a similar but slighter difference, the pollen of the short stamens of the mid-styled form yielding a smaller average of seed during the two years of 1862 and 1863 than that from the short stamens of the long-styled form. Again, if we look to Table I., to the legitimate action of the green pollen of the two sets of long stamens, we shall find exactly the same result, viz. that the pollen of the long stamens of the mid-styled form yielded during both years fewer seeds than that from the long stamens from the short-styled form. Hence it is certain that the two kinds of pollen produced by the mid-styled form are less potent than the similar pollens produced by the corresponding stamens of the two other forms.

When we see that the capsules of the mid-styled form yield a considerably larger average number of seed than those of the other two forms,—when we see how surely the flowers are fertilized in the legitimate unions, and how much more productive

the illegitimate unions are than those of the other two forms, we are led to consider the mid-styled form as eminently feminine in its nature. And although it is impossible to consider as rudimentary or aborted the two perfectly developed sets of stamens of the mid-styled form which produce an abundance of perfectly well-developed pollen, yet we can hardly avoid connecting, as balanced, the higher efficiency of the female organ with the lesser potency of the two mid-styled pollens.

Finally, it is proved by the Tables that *Lythrum salicaria* habitually produces or consists of three females different in structure and widely different in function; that it produces or consists of three sets of males widely different in structure and function; and that two of the three sets of males are subdivided into subgroups of half a dozen each, differing in a marked manner in potency, so that regularly five kinds of pollen are elaborated by this one species of *Lythrum.*

Lythrum Græfferi.—I must now say a few words about some of the other species of the genus. I have examined numerous dried flowers of *L. Græfferi*, each from a separate plant, kindly sent me from Kew. This species, like *L. salicaria*, is trimorphic, and the three forms apparently occur in about equal numbers. In the long-styled form the pistil projects about one-third of the length of the calyx beyond its mouth, and is therefore shorter than in *L. salicaria*; the globose and hirsute stigma is larger than that of the other two forms; the longer stamens, which are graduated in length, have their anthers standing just above and just beneath the mouth of the calyx; the half-dozen shorter stamens rise rather above the middle of the calyx. In the mid-styled form the stigma projects just above the mouth of the calyx, and stands almost on a level with the longer stamens of the previous form; its own longer stamens project well above the mouth of the calyx and stand a little above the level of the stigma of the long-styled form; the shorter stamens correspond in all respects with the shorter ones in the previous form. In the short-styled form the stigma of the pistil is nearly on a level with the anthers of the shorter stamens in the two preceding forms; and the longer stamens correspond with the longer stamens of the mid-styled form, and the shorter stamens with the longer stamens of the long-styled form. In short, there is a close general correspondence in structure between this species and *L. salicaria*, but with some differences in the proportional lengths of the parts. Nevertheless the fact of each of the three pistils having two sets

of stamens, borne by the two other forms, of corresponding lengths, comes out conspicuously. In the mid-styled form the distended pollen-grains from the longer stamens had nearly double the diameter of those from the shorter stamens; so that there is a greater difference in this respect than in *L. salicaria.* In the long-styled form, also, the difference in diameter between the pollen-grains of the longer and shorter stamens was plainer than in *L. salicaria.* These comparisons, however, must be received with caution, as they were made on specimens long kept in a dried condition.

Lythrum thymifolia.—This form, according to Vaucher*, is dimorphic like *Primula*, and therefore presents only two forms. I received two dried flowers from Kew, which presented two forms: in the one form the stigma projected far beyond the calyx, in the other it was included within the calyx; in this latter form the style was only one-fourth of the length of the style of the other form. There are only six stamens; these are somewhat graduated in length, and in the short-styled form the anthers stand a little above the stigma, but yet the stamens by no means equal in length the pistil of the long-styled form; in the long-styled form the stamens are rather shorter than in the other form. These six stamens alternate with the petals, and correspond homologically with the longer stamens of *L. salicaria* and *L. Græfferi.* As there are only six stamens, it is scarcely possible that this species can be trimorphic.

Lythrum hyssopifolia.—This species is said by Vaucher, but I believe erroneously, to be dimorphic. I have examined dried flowers from twenty-two separate plants from various localities, kindly sent to me by Mr. Hewett C. Watson, Prof. Babington, and others. These were all essentially alike. Hence the species cannot be dimorphic. The pistil varies somewhat in length, but when unusually long the stamens are likewise generally long; in the bud the stamens are short: perhaps these circumstances deceived Vaucher. There are from six to nine stamens, graduated in length; the stamens which are variable in being present or absent correspond with the six shorter stamens of *L. salicaria* and with the six which are absent in *L. thymifolia.* The stigma is included within the calyx, and stands in the midst of the anthers, and would generally be fertilized by them; but as the stigma and anthers are upturned, and as, according to Vaucher, there is a passage left in the upper side of the flower to the nectary, there can hardly be a doubt that

* Hist. Phys. des Plantes d'Europe, tom. ii. (1841) pp. 369, 371.

the flowers are visited by insects, which would occasionally bring pollen from other flowers of the same or of any adjoining plant, as surely as occurs with the short-styled *L. salicaria*, of which the pistil and corresponding stamens closely resemble those of *L. hyssopifolia*. According to Vaucher and Lecoq*, this species, which is an annual, generally grows almost solitarily, whereas the three preceding species are social; and this alone would almost have convinced me that *L. hyssopifolia* cannot be dimorphic, as such plants cannot habitually live by themselves any better than one sex of a diœcious species.

Nesæa verticillata.—I raised a number of plants from seed sent me by Professor Asa Gray, and they presented three forms. These differed from each other in the proportional lengths of their organs of fructification and in all respects in very nearly the same way as the three forms of *Lythrum Græfferi*. The green pollen-grains from the longest stamens, measured along their greater axis and not distended with water, were $\frac{13}{7000}$ of an inch in length; those from the stamens of middle length $\frac{9\text{-}10}{7000}$, and those from the shortest stamens $\frac{8\text{-}9}{7000}$ of an inch.

We have seen that the genus *Lythrum* affords trimorphic, dimorphic, and monomorphic species.

The inquiry naturally arises, why do these species differ so remarkably in their sexual relations? of what service can reciprocal dimorphism or trimorphism be to certain species, whilst other species of the same genus present, like the great majority of plants, only one form? I have elsewhere given too briefly † the

* Géograph. Bot. de l'Europe, tom. vi. (1857) p. 157.

† 'Origin of Species,' 3rd edit., p. 101. Hugo von Mohl has recently (Bot. Zeitung, 1863, S. 309, 321), in a most interesting paper, advanced the case of the minute, imperfectly developed, closed and self-fertile flowers borne by *Viola*, *Oxalis*, *Impatiens*, *Campanula*, &c., as an argument against my doctrine that no species is self-fertilized for perpetuity. I may state that in the spring of 1862 I examined some of these flowers, and saw, though less thoroughly, all that H. von Mohl has so well described. I can add only one remark, which I believe is correct, that in *V. canina* there is an open channel for the pollen-tubes from the extremity of the stigma to the ovarium; for I gently pressed a minute bubble of air repeatedly backwards and forwards from end to end. Though the imperfectly developed and the perfect flowers are so different in structure, it is a rather curious case of correlation, that in the double purple Violet (*V. odorata*) the minute imperfect flowers are double to the very core, so that a section appears like the head of a cabbage when cut through. There can be, as von Mohl asserts, no doubt that these flowers are always self-fertilized; they are moreover specially adapted for this end, as may be seen in the remarkable difference in the shape of the pistil in *V. canina* (and in a less degree in *V. hirta* and the single *V. odorata*) as compared with that of the perfect flower;

general grounds of my belief that with all organic beings distinct individuals at least occasionally cross together, and reciprocal dimorphism is plainly one most efficient means for ensuring this result.

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and in the pollen-tubes which proceed from the grains within the anthers in *V. canina*, and from within the lower anthers of *Oxalis acetosella*, having the wonderful power of directing their course to the stigma. If these plants had produced the minute closed flowers alone, the proof would have been perfect that they could never have crossed with other individuals. I am aware that in some of these cases it has been stated that the perfect flowers never produce any seed; as far as *Amphicarpæa* is concerned, I hear from Professor Asa Gray that the petaliferous flowers certainly sometimes yield seed. The completely enclosed flowers of that curious grass, the *Leersia oryzoides*, as described by M. Duval-Jouve (Bull. Soc. Bot. de France, tom. x. 1863, p. 194), apparently offer the best case of perpetual self-fertilization; for when perfect flowers are protruded from the culms, they are, as far as is yet known, always sterile. In a number of plants kept by me in pots in water, not one single perfect flower has protruded, but the enclosed flowers produced plenty of seed. Without wishing to throw any doubt on M. Duval-Jouve's excellent observations, I may add that with the enclosed flowers borne by my plants, the act of fertilization, that is, the penetration of the stigma by the pollen-tubes, took place in the air and not in fluid within the glumes. With the exception of the *Leersia*, as the case now stands, I cannot see how the production of the small, imperfect flowers invalidates my doctrine that no species is perpetually self-fertilized, more than the multiplication of many plants by bulbs, stolons, &c. As I observe that the production of seed by the perfect flowers of *Viola* is spoken of as something capricious and accidental, I may state that, although it varies much in different years, it depends exclusively on the visits of bees; I ascertained this by marking many flowers thus visited, and finding that they produced capsules, and by covering up many flowers which (excepting a few that I artificially fertilized) did not, when thus protected, produce a single capsule. After bees have visited these flowers, the pollen may be seen scattered on the papillæ and on the stigma itself, and they can hardly fail thus to cross distinct individuals. These remarks apply to *V. canina*, *hirta*, and *odorata*; with *V. tricolor* the case is somewhat different; but I must not enlarge any more on this subject. The production by so many plants of perfect and expanded, as well as of imperfect and closed flowers, seems to me to throw much light on many points; it shows how extraordinarily little pollen is necessary for full fertilization, for I ascertained with *V. canina* that the perfect and imperfect flowers (the latter producing so few pollen-grains) yielded the same average number of seeds; it shows us that fertilization can be perfected in closed flowers; it shows us that large, highly coloured petals, perfume, and the secretion of nectar are by no means indispensable for this act, even in those species which properly possess these characters. It seems to me that the necessity of an occasional cross with a distinct individual of the same species explains the universal presence of at least some expanded flowers, at the expense of injury from rain and the loss of much pollen by innumerable pollen-robbing insects; it explains the enormous superfluity of pollen from its liability to loss from these causes and during conveyance from flower to flower; it explains the use of a gaily coloured corolla, perfume, and nectar, namely, to attract insects, except in those comparatively few cases in which wind is the agent, and in these the last-named attributes are deficient.

This result would appear to be one of high importance, for with dimorphic plants it is ensured at the risk of occasional sterility; not only is the pollen of each plant useless or nearly useless to that individual, but so is the pollen of all the plants of the same form, that is, of half the total number of individual plants. In that extensive class of plants called by C. K. Sprengel dichogams, in which the pollen of each flower is shed before its own stigma is ready, or in which the stigma (though this case occurs more rarely) is mature before the flower's own pollen is ready sterility can hardly fail to be the occasional result; and it would be the inevitable result with both dichogamous and reciprocally dimorphic flowers unless pollen were carried by insects (and in some few species by the wind) from one flower or plant to the other. As with reciprocal dimorphism so with dichogamy, within the same genus some of the species are and some are not thus characterized. Again, in the same genus, as in that of *Trifolium*, some species absolutely require insect-aid to produce seed, others are fertile without any such aid; now when insects are requisite for fertilization, pollen will generally be carried from one flower to the other. We thus see, by means of reciprocal dimorphism, of dichogamy, and of insect-aid, that some species require, or at least receive, incessant crosses with other individuals of the same species; whereas other species of the same genera can be, and probably are often fertilized during long periods by the pollen of their own flowers. Why this wide difference in the frequency of crosses should occur we are profoundly ignorant. I will only further remark on this head, that it would be a great mistake to suppose that many flowers, which are neither reciprocally dimorphic nor dichogamous, nor require insect-aid for their fertilization, nor show any particular adaptation in their structure for the visits of insects, are not habitually crossed with the pollen of other individuals; this occurs, for instance, habitually with cabbages, radishes, and onions, which nevertheless are perfectly fertile (as I know by trial) with their own pollen without aid of any kind.

But it may be further asked, granting that reciprocal dimorphism is of service by ensuring at each generation a cross (but I am far from pretending that it may not have some additional unknown signification), why did not dimorphism suffice for *L. salicaria* and *Græfferi*? why were they rendered reciprocally trimorphic, entailing such complicated sexual relations? We cannot answer, except perhaps so far:—if we suppose two plants of

the *L. salicaria* to grow by themselves, then if the species were dimorphic it would only be an equal chance in favour of the two turning out different forms and consequently both being fertile; but as the species is trimorphic and each form can fertilize the two other forms, it is two to one in favour of the two turning out different forms and being consequently both fertile. We thus see how reciprocal trimorphism must be an advantage; and probably it would be more advantageous to this Lythrum, which commonly grows in almost a single row along the banks of streams, than it would be to Primroses or Cowslips which have neighbours on all sides. But even if trimorphism effected no good beyond that gained by dimorphism, we ought not to feel much surprised at its occurrence, for we continually see throughout nature the same end gained by the most complicated as well as by the most simple means: to give one instance:—in many diœcious plants pollen is carried from the male to the female by the wind, which is perhaps the simplest method conceivable, or by the adherence of the grains to the hairy bodies of insects, which is a method only a little less simple; but in *Catasetum* the conveyance is effected by the most complex machinery; for in this orchid we have sensitive horns which when touched cause a membrane to rupture, and this sets free certain springs by which the pollen-masses are shot forth like an arrow, and they adhere to the insect's body by a peculiar viscid matter, and then by the breaking of an elastic thread of the right strength the pollen is left sticking to the stigma of the female plant. The complexity of the means used in this and in many other cases, in fact depends on all the previous stages through which the species has passed, and on the successive adaptations of each part during each stage to changed conditions of life.

As some authors consider reciprocal dimorphism to be the first step towards diœciousness, the difficulty of understanding how a trimorphic plant like *Lythrum salicaria* could become diœcious should be noticed; and as dimorphism and trimorphism are so closely allied, it is not probable that either state is necessarily in any way related to a separation of the sexes—though it may occasionally lead to this end. As far as *Lythrum salicaria* is concerned, the one tendency which we can discover is towards the abortion of the two sets of stamens in the mid-styled form. This tendency is evinced by its pollen, though abundant and apparently good, yielding a smaller percentage of seed than does the pollen of the corresponding stamens in the other two forms; and this

fact is in itself curious, and shows by what insensibly graduated steps nature moves. If this tendency were carried out the mid-styled form would become a female, depending for its fertilization on two sets of stamens in the long- and short-styled forms; and these two forms would reciprocally fertilize each other like the two forms of *Primula* or *Linum*; but there would be no approach to a diœcious condition.

As the case of the trimorphic species of *Lythrum* is so complicated, and as it is easier to perceive the relations of the sexes in the animal than in the vegetable kingdom, it may be worth while to give, before concluding, a somewhat elaborate simile. We may take the case of a species of Ant, and suppose all the individuals invariably to live in three kinds of communities; in the first, a large-sized female (not to specify other differences) living with six middle-sized and six small-sized males; in the second, a middle-sized female with six large- and six small-sized males; and in the third community, a small-sized female with six large- and six middle-sized males. Each one of these three females, though enabled to unite with any male, would be nearly sterile with her own two sets of males, and likewise with two other sets of males living in the other two communities; for she would be fully fertile only when paired with a male of her own size. Hence the thirty-six males, distributed by half-dozens in the three communities, would be divided into three sets of a dozen each; and these sets, as well as the three females, would differ from each other sexually in exactly the same manner as distinct species of the same genus. Moreover the two sets of males living in the community of the extraordinarily fertile middle-sized female would be less potent sexually than the males of corresponding size in the two other communities. Lastly, we should find that from the eggs laid by each of the three females, all three sorts of females and all three sorts of males were habitually reared—proving to demonstration that all belonged to one and the same species.

To appreciate fully this remarkable case of the reciprocally trimorphic species of *Lythrum*, we may take a glance at the two great kingdoms of nature and search for anything analogous. With animals we have the most astonishing diversity of structure in the so-called cases of alternate generation, but as such animals have not arrived at maturity, they are not properly comparable with the forms of *Lythrum*. With mature animals we have extreme differences in structure in the two sexes; we have in

some of the lower animals males, females, and hermaphrodites of the same species; we have the somewhat more curious case of certain Cirripedes which are hermaphrodites, but are sexually aided by whole clusters of what I have called complemental males; we have, as Mr. Wallace has lately shown, the females of certain Lepidoptera existing under three distinct forms; but in *none of these cases is there any reason to suspect that there* is more than one female or one male sexual element. With certain insects, as with Ants, in which there exist, besides males and females, two or three castes of workers, we have a slightly nearer approach to our case, for the workers are so far sexually affected as to have been rendered sterile. With plants, at least with phanerogamic plants, we have not that wonderful series of successive developmental forms so common with animals; nor could this be expected, as plants are fixed to one spot from their birth, and must be adapted throughout life to the same conditions. With plants we have sexual differences in structure, but apparently less strongly marked than with animals, from causes which are in part intelligible, such as there being no sexual selection; again, we have that class of dimorphic flowers so ably discussed recently by Hugo von Mohl, in which some of the flowers are minute, imperfectly developed, and necessarily self-fertile, whilst others are perfect and capable of crossing with other flowers of the same species; but in these several cases we have no reason to suspect that there is more than one female or one male sexual element. When we come to the class of reciprocally dimorphic plants, such as *Primula, Linum,* &c., we first meet with two masculine and two feminine sexes. But these cases, which seemed only a short time since so strange, now sink almost into insignificance before that of the trimorphic species of *Lythrum.*

Naturalists are so much accustomed to behold great diversities of structure associated with the two sexes, that they feel no surprise at the fact; but differences in sexual nature have been thought to be the very touchstone of specific distinction. We now see that such sexual differences—the greater or less power of fertilizing and being fertilized—may characterize and keep separate the coexisting individuals of the same species, in the same manner as they characterize and have kept separate those groups of individuals, produced from common parents during the lapse of ages or in different regions, which we rank and denominate as distinct species.

[*From the* Annals and Magazine of Natural History *for September* 1869.]

NOTES

ON

THE FERTILIZATION OF ORCHIDS.

BY

CHARLES DARWIN, M.A., F.R.S.

To the Editors of the Annals and Magazine of Natural History.

Gentlemen,

Having drawn up some notes for a French translation of my work 'On the various contrivances by which British and Foreign Orchids are Fertilized by Insects' (1862), it has appeared to me that these notes would be worth publishing in English. I have thus been able to bring up the literature of the subject to the present day, by giving references to, together with very brief abstracts of, all the papers published since my work appeared. These papers contain, on the one hand, corrections of some serious errors into which I had fallen, and, on the other hand, confirmations of many of my statements. I have also been able to add, from my own observations and those of others, a few new facts of interest. A heading is given to each note, which will show the nature of the correction or addition, without any reference to my book; but I have added in a parenthesis the page to which the note ought to be appended.

Gentlemen,
Your obedient Servant,
Charles Darwin.

Down, Beckenham, Kent.
July 23, 1869.

Orchis or *Anacamptis pyramidalis* (p. 20).—The late Prof. Treviranus has confirmed (Botanische Zeitung, 1863, p. 241) my observations on this remarkable species; but he differs from me in one or two minor points.

On the kinds of Insects which habitually visit and fertilize some of the common British species of Orchis (p. 35).—I believe

that it may be safely predicated that orchids with very long nectaries, such as the *Anacamptis*, *Gymnadenia*, and *Platanthera*, are habitually fertilized by Lepidoptera, whilst those with only moderately long nectaries are fertilized by bees and Diptera—in short, that the length of the nectary is correlated with that of the proboscis of the insect which visits the plant. I have now seen *Orchis morio* fertilized by various kinds of bees, namely:—by the hive-bee (*Apis mellifica*), to some of which from ten to sixteen pollen-masses were attached; by *Bombus muscorum*, with several pollen-masses attached to the bare surface close above the mandibles; by *Eucera longicornis*, with eleven pollen-masses attached to its head; and by *Osmia rufa*. These bees, and the other Hymenoptera mentioned throughout these notes, have been named for me by our highest authority, Mr. Frederick Smith, of the British Museum. The Diptera have been named by Mr. F. Walker, of the same establishment. In Northern Germany, Dr. H. Müller of Lippstadt found pollen-masses of *Orchis morio* attached to *Bombus silvarum*, *lapidarius*, *confusus*, and *pratorum*. The same excellent observer found the pollen-masses of *Orchis latifolia* attached to a *Bombus*; but this orchis is also frequented by Diptera. A friend watched for me *Orchis mascula*, and saw several flowers visited by a *Bombus*, apparently *B. muscorum*; but it is surprising how seldom any insect can be seen visiting this common species. With respect to *Orchis maculata*, my son, Mr. George Darwin, has clearly made out the manner of its fertilization. He saw many specimens of a fly (*Empis livida*) inserting their proboscides into the nectary; and subsequently I saw the same occurrence. He brought home six specimens of this *Empis*, with pollinia attached to their spherical eyes, on a level with the bases of the antennæ. The pollinia had undergone the movement of depression, and stood a little above and parallel to the proboscis: hence they were in a position excellently adapted to strike the stigma. Six pollinia were thus attached to one specimen, and three to another. My son also saw another and smaller species (*Empis pennipes*) inserting its proboscis into the nectary; but this species did not act so well or so regularly as the other in fertilizing the flowers. One specimen of this latter *Empis* had five pollinia, and a second had three pollinia, attached to the dorsal surface of the convex thorax.

On nectar being secreted and contained between the outer and inner membranes of the nectary in several species of Orchis (p. 51).—I have repeated my observations on the nectaries of some of our common species, and especially on those of *Orchis morio, at the time when various bees were continually visiting*

the flowers; but I could never see the minutest drop of nectar within the nectary. Each bee remained a considerable time with its proboscis in constant movement whilst inserted into the nectary. I observed the same fact with *Empis* in the case of *Orchis maculata*; and in this orchis I could occasionally detect minute brown specks, where punctures had been made. Hence the view suggested by me that insects puncture the inner lining of the nectary and suck the fluid contained between the two coats may be safely accepted. I have said in my work that this hypothesis was a bold one, as no instance was known of Lepidoptera penetrating with their delicate proboscides any membrane; but I now hear from Mr. R. Trimen that at the Cape of Good Hope moths and butterflies do much injury to peaches and plums by penetrating the skin, in parts which have not been in the least broken.

Since the appearance of my work, the following observations have been published on other species of Orchis *and on certain allied forms* (p. 53).—Mr. J. Traherne Moggridge has given (Journ. Linn. Soc. vol. viii. Botany, 1865, p. 256) a very interesting account of the structure and manner of fertilization of *Orchis* or *Aceras longibracteata.* Both pollinia, as in *Anacamptis pyramidalis*, are attached to the same viscid disk; but, differently from those in that species, after being removed from the anther-cases, they first converge and then undergo the movement of depression. But the most interesting peculiarity in this species is that insects suck nectar out of minute open cells in the honeycombed surface of the labellum. Mr. Moggridge saw this plant fertilized by a large bee, the *Xylocopa violacea.* He adds some observations on *Orchis hircina*, and describes the structure and manner of fertilization of *Serapias cordigera* by another bee, viz. the *Ceratina albilabris.* In this *Serapias* both pollinia are attached to the same viscid disk; when first withdrawn, they are bent backwards, but soon afterwards move forwards and downwards in the usual manner. As the stigmatic cavity is narrow, the pollinia are guided into it by two guiding plates.

Mr. Moggridge sent me from Northern Italy living plants of *Orchis* or *Neotinea intacta*, together with excellent drawings and a full account of the structure of the flower. He informed me that this species is remarkable for producing seed without the aid of insects; and I ascertained that when insects were carefully excluded, almost all the flowers produced capsules. Their fertilization follows from the pollen being extremely incoherent, and spontaneously falling on the stigma. Nevertheless a short nectary is present, the pollinia possess

small viscid disks, and all the parts are so arranged that, if insects were to visit the flowers, the pollen-masses would probably be removed and then carried to another flower, but not so effectually as with most other orchids. We shall hereafter find a few other cases of orchids which have structural peculiarities adapted both for self-fertilization and for crossing. I may here also refer to a paper by Mr. R. Trimen (Journ. Linn. Soc. vol. vii. Botany, 1863, p. 144) on the beautiful *Disa grandiflora* of the Cape of Good Hope. This orchid presents several remarkable characteristics, one of these being that the pollinia do not spontaneously undergo any movement of depression, the weight of the pollen-masses sufficing to bend the caudicle into the proper curvature for the act of fertilization. Another peculiarity is that the posterior sepal secretes nectar, and is developed into a spur-like nectary. Mr. Trimen informs me that he has seen a Dipterous insect, allied to *Bombylius*, frequenting the flowers. I may add that Mr. Trimen has sent me descriptions and specimens of various other South-African orchids, which confirm the general conclusions at which I have arrived in my work.

On the movement of the pollinia of Ophrys muscifera (p. 56).—Mr. T. H. Farrer, who has lately been attending to the fertilization of various plants, has convinced me that I have erred, and that the pollinia of this *Ophrys* do undergo a movement of depression. Hence my remarks on the correlation of the various parts of the flower are to a certain extent invalidated; but there can be no doubt that the naturally bent caudicle plays an important part in placing the pollen-mass in a proper position for striking the stigma. I have continued occasionally to watch the flowers of this species, but have never succeeded in seeing insects visit them; but I have been led to suspect that they puncture or gnaw the small lustrous prominences beneath the viscid disks, which, I may add, are likewise present in several allied species. I have observed very minute punctures on these prominences, but I could not decide whether these had been made by insects or whether superficial cells had spontaneously burst.

Ophrys aranifera (p. 63).—F. Delpino states (Fecondazione nelle Piante &c., Firenze, 1867, p. 19) that he has examined in Italy thousands of specimens of this *Ophrys*, and that it seldom produces capsules. It does not secrete any nectar. Although he never saw an insect on the flowers (excepting once a green locust), nevertheless they are fertilized by insects; for he found pollen on the stigmas of some flowers, which had their own pollinia still within the anther-cases. The pollinia never

spontaneously fall out. He appears to think that I infer that this *Ophrys* fertilizes itself, which is an error.

Ophrys apifera (p. 71).—Prof. Treviranus at first doubted (Botanische Zeitung, 1862, p. 11) the accuracy of my account of this *Ophrys*, and of the differences between it and *O. arachnites*; but he has subsequently (Bot. Zeit. 1863, p. 241) fully confirmed all that I have stated.

Ophrys arachnites (p. 72).—I have now examined several additional living specimens of this *Ophrys*, and can confirm my statement that the pollinia do not fall out of the anther-cases, even when the spikes are strongly shaken; nor do they fall out when the spikes are kept standing in water for a week. Mr. J. Moggridge has made (Journ. Linn. Soc., Bot. vol. viii. 1865, p. 258) a remarkable observation on *O. scolopax*, which is closely allied to *O. arachnites*,—namely, that at Mentone it never exhibits any tendency to self-fertilization, whilst at Cannes all the flowers fertilize themselves, owing to a slight modification in the curvature of the anther, which causes the pollinia to fall out. This botanist has given, in his 'Flora of Mentone,' a full description, with excellent figures, of *O. scolopax*, *arachnites*, *aranifera*, and *apifera*; and he believes, from the number of intermediate forms, that they must all be ranked as varieties of a single species, and that their differences are intimately connected with their period of flowering. It does not appear that these forms in England, judging from their distribution, are liable to pass into each other, within any moderate or observable period of time.

On the fertilization of Herminium monorchis (p. 74).—My son, Mr. George Darwin, has fully observed the manner of fertilization of this minute and rare orchis. It differs from that of any other genus known to me. He saw the flowers entered by various minute insects, and brought home no less than twenty-seven specimens with pollinia (generally with only one, but sometimes with two) attached to them. These insects consisted of minute Hymenoptera (of which *Tetrastichus diaphantus* was the commonest), of Diptera and Coleoptera, the latter being *Malthodes brevicollis*. The one indispensable point appears to be that the insect should be of very minute size, the largest being only the $\frac{1}{20}$ of an inch in length. It is an extraordinary fact that in all the specimens the pollinia were attached to the same peculiar spot, namely, to the outer side of one of the two front legs, to the projection formed by the articulation of the femur with the coxa. In one instance alone a pollinium was attached to the outside of the femur a little beneath the articulation. The cause of this peculiar manner of attachment is sufficiently clear: the middle part

of the labellum stands so close to the anther and stigma, that insects always enter the flower at one corner, between the margin of the labellum and one of the upper petals; they also almost always crawl in with their backs turned directly or obliquely towards the labellum. My son saw several which had begun to crawl into the flower in a different position; but they came out and changed their position. Thus, standing in either corner of the flower, with their backs turned towards the labellum, they inserted their heads and fore legs into the short nectary, which is seated between the two widely separated viscid disks. I ascertained that they stand in this position by finding three dead insects, which had been permanently glued to the disks. Whilst sucking the nectar, which occupies about two or three minutes, the projecting joint of the femur stands under the large helmet-like viscid disk on either side; and when the insect retreats, the disk exactly fits on, and is glued to, the prominent joint. The movement of depression in the caudicle then takes place, and the mass of pollen-grains projects just beyond the tibia; so that the insect, when entering another flower, can hardly fail to fertilize the stigma, which is situated directly beneath the disk on either side. I know of hardly any other case in which the whole structure of the flower is more beautifully correlated than in the *Herminium* for a most peculiar manner of fertilization.

On the movement of the pollinia in Peristylus viridis (p. 76).—Mr. T. H. Farrer informs me that the pollinia certainly undergo a movement of depression, but that this does not take place until twenty or thirty minutes have elapsed after their removal from the anther-cases. This length of time probably accounts for my oversight. He asserts that, after the movement of depression, the pollinia become much better adapted to strike the stigmatic surface. He suggests that insects may take a long time to lick up the nectar from the two naked spots on the labellum, and through the narrow slit-like opening into the nectary—and that during this time the pollinium becomes firmly attached, by the slow hardening of the viscid matter, to the insect's body, so as to be subsequently ready to fertilize another flower when visited by the same insect.

On the Lepidoptera which fertilize the Gymnadenia conopsea, *and on the divergence of the pollinia* (p. 82).—Mr. George Darwin went at night to a bank where this species grows plentifully, and soon caught *Plusia chrysitis* with six pollinia, *P. gamma* with three, *Anaitis plagiata* with five, and *Triphæna pronuba* with seven pollinia attached to their proboscides.

I may add that he caught the first-named moth, bearing the pollinia of this orchis, in my flower-garden, although more than a quarter of a mile distant from any spot where the plant grows. I state in my work that I do not understand the cause of the divergence of the pollinia so that they are enabled to strike the lateral stigmatic surfaces; but the explanation is simple. The upper margin of the nectary is arched, being formed on one side by the disk of one pollinium, and on the other side by the other disk. Now if a moth inserts its proboscis obliquely, and there are no guiding-ridges by which, as in *Anacamptis pyramidalis*, a moth is compelled to insert its proboscis directly in front, or if a bristle be inserted obliquely, one pollinium alone is removed. In this case the pollinium becomes attached a little on one side of the bristle or proboscis; and its extremity, after the vertical movement of depression, occupies a proper position for striking the lateral stigma on the same side.

On the Gymnadenia tridentata *of North America* (p. 83).—Prof. Asa Gray has published (American Journal of Science, vol. xxxiv. 1862, p. 426, and footnote p. 260; and vol. xxxvi. 1863, p. 293) some interesting notes on the *Gymnadenia tridentata*. The anther opens in the bud, and some of the pollen invariably falls on the naked cellular tip of the rostellum; and this part, strange to say, is penetrated by the pollen-tubes, so that the flowers are self-fertilized. Nevertheless "all the arrangements for the removal of the pollinia by insects (including the movement of depression) are as perfect as in the species which depend upon insect aid." Hence there can be little doubt that this species is occasionally crossed.

Habenaria or *Platanthera bifolia* (p. 88).—According to Dr. H. Müller, of Lippstadt, *Pl. bifolia* of English authors is the *Pl. solstitialis* of Boenninghausen; and he fully agrees with me that it must be ranked as specifically distinct from *Pl. chlorantha*. Dr. Müller states that this latter species is connected by a series of gradations with another form which in Germany is called *Pl. bifolia*. He gives a very full and valuable account of the variability of these species of *Platanthera* and of their structure in relation to their manner of fertilization. (See Verhandl. d. Nat. Verein. Jahrg. xxv. III. Folge, v. Bd. pp. 36–38.)

American species of Platanthera (p. 91).—Prof. Asa Gray has described (American Journal of Science, vol. xxxiv. 1862, pp. 143, 259, & 424, and vol. xxxvi. 1863, p. 292) the structure of ten American species of *Platanthera*. Most of these resemble in their manner of fertilization the two British species described by me; but some of them, in which the viscid

disks do not stand far apart, have curious contrivances, such as a channelled labellum, lateral shields, &c., compelling moths to insert their proboscides directly in front. *Pl. Hookeri*, on the other hand (*ibid.* vol. xxxiv. 1862, p. 143), differs in a very interesting manner: the two viscid disks stand widely separated from each other; consequently a moth, unless of gigantic size, would be able to suck the copious nectar without touching either disk; but this risk is avoided in the following manner:—The central line of the stigma is prominent, and the labellum, instead of hanging down, as in most of the other species, is curved upwards, so that the front of the flower is made somewhat tubular and is divided into two halves. Thus a moth is compelled to go to one or the other side, and its face will almost certainly be brought into contact with one of the disks. The drum of the pollinium, when removed, contracts in the same manner as I have described under *Pl. chlorantha*. Prof. Gray has seen a butterfly from Canada with the pollinia of this species attached to each eye. In the case of *Platanthera flava* (American Journal of Science, vol. xxxvi. 1863, p. 292), moths are compelled in a different manner to enter the nectary on one side. A narrow but strong protuberance, rising from the base of the labellum, projects upwards and backwards, so as almost to touch the column; thus the moth, being forced to go to either side, is almost sure to withdraw one of the viscid disks. In the allied and wonderful *Bonatea speciosa* of the Cape of Good Hope there is a similar contrivance for the same purpose.

Platanthera hyperborea and *dilatata* have been regarded by some botanists as varieties of the same species; and Prof. Asa Gray says (Amer. Journ. of Science, vol. xxxiv. 1862, pp. 259 & 425) that he has often been tempted to come to the same conclusion; but now, on closer examination, he finds, besides other characters, a remarkable physiological difference, namely, that *Pl. dilatata*, like its congeners, requires insect aid and cannot fertilize itself; whilst in *Pl. hyperborea* the pollen-masses commonly fall out of the anther-cells whilst the flower is very young or in bud, and thus the stigma is self-fertilized. Nevertheless the various structures adapted for crossing are still present.

Fertilization of Epipactis palustris (p. 102).—My son, Mr. W. E. Darwin, has carefully observed for me this plant in the Isle of Wight. Hive-bees seem to be the chief agents in fertilization; for he saw about a score of flowers visited by these insects, many of which had pollen-masses attached to their foreheads, just above the mandibles. I had supposed that insects crawled into the flowers; but hive-bees are too large to

do this; they always clung, whilst sucking the nectar, to the distal and hinged half of the labellum, which was thus pressed downwards. Owing to this part being elastic and tending to spring up, the bees, as they left the flowers, seemed to fly rather upwards; and this would favour, in the manner explained by me, the complete withdrawal of the pollen-masses, quite as well as an insect crawling out of the flower in an upward direction. Perhaps, however, this upward movement may not be so necessary as I had supposed; for, judging from the point at which the pollen-masses were attached to the bees, the back part of the head would press against, and thus lift up, the blunt, solid, upper end of the anther, thus freeing the pollen-masses.

Various other insects besides hive-bees visit this *Epipactis*. My son saw several large flies (*Sarcophaga carnosa*) haunting the flowers; but they did not enter in so neat and regular a manner as the hive-bees; nevertheless two had pollen-masses attached to their foreheads. Several smaller flies (*Cœlopa frigida*) were also seen entering and leaving the flowers, with pollen-masses adhering rather irregularly to the dorsal surface of the thorax. Three or four distinct kinds of Hymenoptera (one of small size being *Crabro brevis*) likewise visited the flowers; and three of these Hymenoptera had pollen-masses attached to their backs. Other still more minute Diptera, Coleoptera, and ants were seen sucking the nectar; but these insects appeared to be too small to transport the pollen-masses. It is remarkable that some of the foregoing insects should visit these flowers; for Mr. F. Walker informs me that the *Sarcophaga* frequents decaying animal matter, and the *Cœlopa* haunts seaweed, occasionally settling on flowers; the *Crabro* also, as I hear from Mr. F. Smith, collects small beetles (*Halticæ*) for provisioning its nest. It is equally remarkable, seeing how many kinds of insects visit this *Epipactis*, that, although my son watched for some hours on three occasions hundreds of plants, not a single humble-bee alighted on a flower, though many were flying about. In a footnote I have given the results of experiments made by Mr. More, by cutting off the distal and hinged half of the labellum, in order to ascertain how far this part is important. He has now repeated the experiment on nine additional flowers: of these, three did not produce seed-capsules; but this may have been accidental. Of six capsules which were produced, two contained about as many seeds as the capsules of unmutilated flowers on the same plant; but four capsules contained much fewer seeds. The seeds themselves were well-formed. These experiments, as far as they go, support the view that the distal part of the

labellum plays an important part in leading insects to enter and leave the flower in a proper manner for fertilization.

Fertilization of Epipactis latifolia (p. 104).—Although this orchis is not common in the vicinity of Down, by a fortunate chance several plants sprang up in a gravel walk close to my house, so that I have been able to observe them during several years, and have thus discovered how they are fertilized. Although hive-bees and humble-bees of many kinds were constantly flying over the plants, I never saw a bee or any Dipterous insect visit the flowers; whilst, on the other hand, I repeatedly observed each year the common wasp (*Vespa sylvestris*) sucking the nectar out of the open cup-shaped labellum. I thus saw the act of fertilization effected by the pollen-masses being removed and carried on the foreheads of the wasps to other flowers. Mr. Oxenden also informs me that a large bed of *E. purpurata* (which is considered by some botanists a distinct species, and by others a variety) was frequented by "swarms of wasps." It is very remarkable that the sweet nectar of this *Epipactis* should not be attractive to any kind of bee. If wasps were to become extinct in any district, so would the *Epipactis latifolia.*

Dr. H. Müller of Lippstadt has published (Verhandl. d. Nat. Ver. Jahrg. xxv. III. Folge, v. Bd. pp. 7–36) some very important observations on the differences in structure and in the manner of fertilization, as well as on the connecting gradations, between *Epipactis rubiginosa*, *microphylla*, and *viridiflora.* The latter species is highly remarkable by the absence of a rostellum, and by being regularly self-fertilized. This latter circumstance follows from the incoherent pollen of the lower part of the pollen-masses emitting, whilst still within the anther-cells, pollen-tubes, which penetrate the stigma; and this occurred even in the bud state. This species, however, is probably visited by insects, and occasionally crossed; for the labellum contains nectar. *E. microphylla* is equally remarkable, by being intermediate in structure between *E. latifolia*, which is always fertilized by the aid of insects, and *E. viridiflora*, which does not necessarily require any such aid. The whole of this memoir by Dr. H. Müller deserves to be attentively studied.

Cephalanthera grandiflora (p. 108).—During the year 1862, the flowers of this orchis appeared to have been visited much less frequently by insects than during the previous years; for the masses of pollen were seldom broken down. Although I have repeatedly examined the flowers, I have never seen a trace of nectar; but some appearances lead me to suspect that the ridges within the base of the labellum are attractive to

insects, and are gnawed by them, as in the case of many Vandeæ and other exotic orchids.

Goodyera repens (p. 114).—Mr. R. B. Thomson informs me that in the north of Scotland he saw many humble-bees visiting the flowers and removing the pollen-masses, which were attached to their proboscides. The bee sent was *Bombus pratorum*. This species grows also in the United States; and Prof. Gray (Amer. Journ. of Science, vol. xxxiv. 1862, p. 427) confirms my account of its structure and manner of fertilization, which is likewise applicable to another and very distinct species, namely, *Goodyera pubescens*. Prof. Gray states that the passage into the flower, which is at first very narrow, becomes, as I suspected, more open during its older state. Prof. Gray believes, however, that it is the column, and not the labellum, which changes its position.

Spiranthes autumnalis (p. 123).—As in the case of the *Goodyera*, Prof. Gray feels confident that it is the column which moves from the labellum as the flower grows older, and not, as I had supposed, the labellum which moves from the column. He adds that this change of position, which plays so important a part in the fertilization of the flower, "is so striking that we wonder how we overlooked it" (Amer. Journ. of Science, vol. xxxiv. p. 427).

On the rostellum of Listera ovata *not exploding spontaneously* (p. 149).—I have covered up some additional plants, and found that the rostellum lost its power of explosion in about four days, the viscid matter then turning brown within the loculi of the rostellum. The weather at the time was unusually hot, and this may have hastened the process. After the four days had elapsed, the pollen had become very incoherent and some had fallen on the two corners, or even over the whole surface, of the stigma, which was penetrated by the pollen-tubes. Hence, if insects should fail to remove the pollinia by causing the explosion of the rostellum, this orchid certainly seems capable of occasional self-fertilization. But the scattering of the incoherent pollen was largely aided by, and perhaps wholly depended on, the presence of *Thrips*—insects so minute that they could not be excluded by any net.

Listera cordata (p. 152).—Prof. Dickie has been so good as to observe the flowers on living plants. He informs me that, when the pollen is mature, the crest of the rostellum is directed towards the labellum, and that, as soon as touched, the viscid matter explodes, the pollinia becoming attached to the touching object; after the explosion, the rostellum bends downwards and spreads out, thus protecting the virgin stigmatic surface; subsequently the rostellum rises and exposes

the stigma; so that everything here goes on as I have described under *Listera ovata.* The flowers are frequented by minute Diptera and Hymenoptera.

On the self-fertilization of Neottia nidus-avis, *and on the rostellum not exploding spontaneously* (p. 153).—I covered up with a net several plants, and after four days found that the rostellum had not spontaneously exploded, and had already almost lost this power. The pollen had become incoherent, and in all the flowers much had fallen on the stigmatic surfaces, which were penetrated by pollen-tubes. The spreading of the pollen seemed to be in part caused by the presence of *Thrips*, many of which minute insects were crawling about dusted all over with pollen. The covered-up plants produced plenty of capsules, but these were much smaller and contained much fewer seeds than the capsules produced by the adjoining uncovered plants. I may here add that I detected on the crest of the rostellum some minute rough points, which seemed *particularly* sensitive in causing the rostellum to explode.

Dr. H. Müller, of Lippstadt, informs me that he has seen Diptera sucking the nectar and removing the pollinia of this plant.

On the self-fertilization of certain Epidendreæ (p. 166).—Dr. Crüger says (Journ. Linn. Soc. vol. viii. Botany, 1864, p. 131) that "we have in Trinidad three plants belonging to the Epidendreæ (a *Schomburgkia*, *Cattleya*, and *Epidendron*) which rarely open their flowers, and are invariably impregnated when they do open them. In these cases it is easily seen that the pollen-masses have been acted on by the stigmatic fluid, and that the pollen-tubes descend from the pollen-masses *in situ* down into the ovarian canal." Mr. Anderson, a skilful cultivator of orchids in Scotland, informs me (see also 'Cottage Gardener,' 1863, p. 206) that with him the flowers of *Dendrobium cretaceum* never expand, and yet produce capsules with plenty of seed, which, when examined by me, was found to be perfectly good. These orchids make a near approach to those dimorphic plants (as *Oxalis*, *Ononis*, and *Viola*) which habitually produce open and perfect, as well as closed and imperfect flowers.

On the slow movement of the pollinia in Oncidium (p. 189).—Mr. Charles Wright, in a letter to Prof. Asa Gray, states that he observed in Cuba a pollinium of an *Oncidium* attached to a *Bombus*, and he concluded at first that I was completely mistaken about the movement of depression; but after several hours the pollinium moved into the proper position for fertilizing the flower.

Manner of fertilization of various exotic Orchids (p. 189).

—I may here remark that Delpino (Fecondazione nelle Piante, Firenze, 1867, p. 19) says he has examined flowers of *Vanda*, *Epidendron*, *Phaius*, *Oncidium*, and *Dendrobium*, and confirms my general statements. The late Prof. Bronn, in his German translation of this work (1862, p. 221), gives a description of the structure and manner of fertilization of *Stanhopea devoniensis*.

Sexes of Acropera *not separated* (p. 206).—I have committed a great error about this genus, in supposing that the sexes were separate. Mr. J. Scott, of the Royal Botanic Garden of Edinburgh, soon convinced me that it was an hermaphrodite, by sending me capsules containing good seed, which he had obtained by fertilizing some flowers with pollen from the same plant. He succeeded in doing this by cutting open the stigmatic chamber, and inserting the pollen-masses. My error arose from my ignorance of the remarkable fact that, as shown by Dr. Hildebrand (Botanische Zeitung, 1863, Oct. 30 *et seq.*, and Aug. 4, 1865), in many orchids the ovules are not developed until several weeks or even months after the pollen-tubes have penetrated the stigma. No doubt if I had examined the ovaria of *Acropera* some time after the flowers had withered, I should have found well-developed ovules. In many exotic orchids besides *Acropera* (namely, in *Gongora*, *Cirrhæa*, *Acineta*, *Stanhopea*, &c.), the entrance into the stigmatic chamber is so narrow that the pollen-masses cannot be inserted without the greatest difficulty. How fertilization is effected in these cases is not yet known. That insects are the agents there can be no doubt; for Dr. Crüger saw a bee (*Euglossa*) with a pollinium of a *Stanhopea* attached to its back; and bees of the same genus continually visit *Gongora*. Fritz Müller has observed, in the case of *Cirrhæa* (Bot. Zeitung, Sept. 1868, p. 630), that if one end of the pollen-mass be inserted into the narrow entrance of the stigmatic chamber, this part, from being bathed by the stigmatic fluid, swells, and the whole pollen-mass is thus gradually drawn into the stigmatic entrance. But, from observations which I have made on *Acropera* and *Stanhopea* in my own hot-house, I suspect that, with many of these orchids, the pedicel with the narrow end of the pollinium, and not the broad end, is ordinarily inserted into the stigmatic chamber. By thus placing the pollinium, I have occasionally succeeded in fertilizing some of these orchids, and have obtained seed-capsules.

Structure and fertilization of the Vandeæ *&c. of Brazil* (p. 210).—Fritz Müller has sent me many letters containing an astonishing number of new and curious observations on the structure and manner of cross-fertilization of various orchids

inhabiting South Brazil. I much regret that I have not here space or time to give an abstract of his many discoveries, which support the general conclusions given in my work; but I hope that he will some day be induced to publish a full account of his observations.

Fertilization of Catasetum (p. 211).—It has been highly satisfactory to me that my observations and predictive conclusions in regard to *Catasetum* have been fully confirmed by the late Dr. Crüger, the Director of the Botanic Gardens of Trinidad, in letters to me and in his paper in the 'Journal of the Linnean Society' (vol. viii. Bot. 1864, p. 127). He sent me specimens of the bees, belonging to three species of *Euglossa*, which he saw gnawing the inside of the labellum. The pollinia, when ejected, become attached to, and lie flat on, the backs of the bees, on the hairy surface of the thorax. Dr. Crüger has also proved that I was correct in asserting that the sexes of *Catasetum* are separate, for he fertilized female flowers with pollen from the male plants; and Fritz Müller effected the same thing with *Catasetum mentosum* in South Brazil. Nevertheless, from two accounts which I have received, it appears that *Catasetum tridentatum*, though a male plant, occasionally produces seed-capsules; but every botanist knows that this occasionally occurs with the males of other diœcious plants. Fritz Müller has given (Botanische Zeitung, Sept. 1868, p. 630) a most interesting account, agreeing with mine, of the state of the minute pollinia in the female plant: the anther never opens, and the pollen-masses are not attached to the viscid disks, so that they cannot be removed by any natural means. The pollen-grains, as so generally occurs with rudimentary organs, are extremely variable in size and shape. Nevertheless the grains of the rudimentary pollen-masses belonging to the female plant, when applied (which can never naturally occur) to the stigmatic surface, emitted their pollen-tubes! This appears to me a very curious instance of the slow and gradual manner in which structures are modified; for the female pollen-masses, included within an anther which never opens, are seen still partially to retain their former powers and function.

Mormodes luxatum (p. 265).—I have now examined another species of *Mormodes*, the rare *M. luxatum*, and I find that the chief points of structure, and the action of the different parts, including the sensitiveness of the filament, are the same as in *M. ignea*. The cup of the labellum, however, is much larger, and is not pressed down firmly on the filament on the summit of the column. This cup probably serves to attract insects, and, as in *Catasetum*, is gnawed by them. The flowers

are asymmetrical to an extraordinary degree, the right-hand and left-hand sides differing much in shape.

Cycnoches ventricosum (p. 265).—The plant described in my work as a second species of *Mormodes* proves to be *Cycnoches ventricosum*. I first received from Mr. Veitch some flower-buds, from which the section (fig. xxx.) was taken; but subsequently he sent me some perfect flowers. The yellowish-green petals and sepals are reflexed; the thick labellum is singularly shaped, with its upper surface convex, like a shallow basin turned upside down. The thin column is of extraordinary length, and arches like the neck of a swan over the labellum; so that the whole flower presents a very singular appearance. In the section of the flower, given in my work, we see the elastic pedicel of the pollinium bowed, as in *Catasetum* or *Mormodes*; but at the period of growth represented in the figure the pedicel was still united to the rostellum, the future line of separation being shown by a layer of hyaline tissue indistinct towards the upper end of the disk. The disk is of gigantic size, and its lower end is produced into a great fringed curtain, which hangs in front of the stigmatic chamber. The viscid matter of the disk sets hard very quickly, and changes colour. The disk adheres to any object with surprising strength. The anther is very different in shape from that of *Catasetum* or *Mormodes*, and apparently would retain the pollen-masses with greater force. A part of the filament of the anther, lying between two little leaf-like appendages, is sensitive; and when this part is touched, the pollinium is swung upwards, as in *Mormodes*, and with sufficient force, if no object stands in the way, to throw it to the distance of an inch. An insect of large size alights probably on the labellum, for the sake of gnawing the convex surface, or perhaps on the extremity of the arched and depending column, and then, by touching the sensitive point, causes the ejection of the pollen-masses, which are affixed to its body and thus transported to another flower or plant.

Fertilization of the Arethuseæ (p. 269).—*Epipogium Gmelini* has been the subject of an admirable memoir (Ueber den Blüthenbau, &c., Göttingen, 1866) by Dr. P. Rohrbach, who has shown how the flowers are fertilized by *Bombus lucorum*. With respect to another genus belonging to this same tribe, namely *Pogonia*, Dr. Scudder of the United States has described (Proc. Boston Nat. Hist. Soc. vol. ix. 1863, p. 182) the manner in which it is fertilized by the aid of insects.

Cypripedium (p. 274).—Prof. Asa Gray, after examining several American species of *Cypripedium*, wrote to me (see also Amer. Journ. of Science, vol. xxxiv. 1862, p. 427) that

he was convinced that I was in error, and that the flowers are fertilized by small insects entering the labellum through the large opening on the upper surface, and crawling out by one of the two small orifices close to either anther and the stigma. Accordingly I caught a very small bee which seemed of about the right size, namely the *Andrena parvula* (and this by a strange chance proved, as we shall presently see, to be the right genus), and placed it in the labellum through the upper large opening. The bee vainly endeavoured to crawl out again the same way, but always fell backwards, owing to the margins being inflected. The labellum thus acts like one of those conical traps with the edges turned inwards, which are sold to catch beetles and cockroaches in the London kitchens. Ultimately the little bee forced its way out through one of the small orifices close to one of the anthers, and was found when caught to be smeared with the glutinous pollen. I then again put the same bee into the labellum; and again it crawled out through one of the small orifices. I repeated the operation five times, always with the same result. I then cut away the labellum, so as to examine the stigma, and found it well smeared over with pollen. Delpino (Fecondazione &c. 1867, p. 20) with much sagacity foresaw that some insect would be discovered to act in the manner just described; for he argued that if an insect were to insert its proboscis, as I had supposed, from the outside through one of the small orifices close to one of the anthers, the stigma would be fertilized by the plant's own pollen; and in this he did not believe, from having confidence in what I have often insisted on—namely, that all the contrivances for fertilization are arranged so that the stigma shall receive pollen from a distinct flower or plant. But these speculations are now all superfluous; for, owing to the admirable observations of Dr. H. Müller, of Lippstadt (Verh. d. Nat. Ver. Jahrg. xxv. III. Folge, v. Bd. p. 1), we actually know that *Cypripedium calceolus* in a state of nature is fertilized by two species of *Andrena*, in the manner above supposed.

On the relation between the more or less viscid condition of the pollen and stigma in Cypripedium (p. 276).—The relation between the state of the pollen and stigma, which I have pointed out in my work, is strongly confirmed by Prof. Gray's statement (Amer. Journ. of Science, vol. xxxiv. 1862, p. 428), namely, that in *C. acaule* the pollen is much more granular or less viscid than in other American species of the genus, and in this species alone the stigma is slightly concave and viscid! Dr. Gray adds that in most of the species the broad stigma presents another remarkable peculiarity, "in being closely

beset with minute, rigid, sharp-pointed papillæ, all directed forwards, which are excellently adapted to brush off the pollen from an insect's head or back."

The use of the copious fluid contained within the labellum of Coryanthes (p. 278).—The *Coryanthes macrantha* is perhaps the most wonderful of all known orchids, even more wonderful in structure and function than *Catasetum*. Its manner of fertilization has been described by Dr. Crüger in the 'Journal of the Linnean Society' (vol. viii. Bot. 1864, p. 130), and in letters to me. He sent me bees, belonging to the genus *Euglossa*, which he saw at work. The fluid in the bucket formed by the basal part of the labellum is not nectar and does not attract insects, but serves, by wetting their wings, to prevent them from crawling out except through the small passages close to the anther and stigma. Thus the secretion of fluid in this orchis serves exactly the same end as the inflected margins of the labellum in *Cypripedium*.

On the evidence that Insects visit many exotic Orchids in order to gnaw parts of the labellum, and not for the sake of nectar (p. 284).—It has been highly satisfactory to me that this hypothesis has been fully confirmed. In the West Indies, Dr. Crüger witnessed humble-bees of the genus *Euglossa* gnawing the labellum of *Catasetum*, *Coryanthes*, *Gongora*, and *Stanhopea*; and Fritz Müller has repeatedly found, in South Brazil, the prominences on the labellum of *Oncidium* gnawed. We are thus enabled to understand the meaning of the various extraordinary crests and projections on the labellum of various exotic orchids; for they invariably stand in such a position that insects, whilst gnawing them, will be almost sure to touch the viscid disks of the pollinia, and thus remove them.

Bonatea speciosa (p. 305).—The manner of fertilization of this extraordinary orchis has now been fully described by Mr. R. Trimen in the 'Journal of the Linnean Society' (vol. ix. Bot. 1865, p. 156). A projection rising from the base of the labellum is one of its most remarkable peculiarities, as an insect is thus compelled to insert its proboscis on one side, and thus to touch one of the two widely separated and projecting viscid disks. Mr. J. P. Mansel Weale has also published (*ibid.* vol. x. 1869, p. 470) analogous observations on a second species, viz. *Bonatea Darwinii*. Mr. Weale caught a skipper-butterfly (*Pyrgus elmo*) quite embarrassed by the number of pollinia belonging to this orchis which adhered to its sternum. I do not know of any other case in which the pollinia adhere to the sternum of a Lepidopterous insect.

On the nature of the contraction which causes the pollinia, after their removal from the anther, to change their position

(p. 338).—In *Orchis hircina*, I clearly saw, under the microscope, the whole front of the viscid disk become depressed as the two pollinia together underwent the movement of depression.

Number of seeds (p. 344).—The number of seeds produced by *Orchis maculata*, as given in my work, is small in comparison with that produced by some foreign species. I have shown (Variation of Animals and Plants under Domestication, vol. ii. 1868, p. 379), on the authority of Mr. Scott, that a single capsule of *Acropera* contained 371,250 seeds; and the species produces so many flowers and racemes, that a single plant probably sometimes produces as many as 74 millions of seeds in the course of a single year. Fritz Müller carefully estimated, by weighing, the number of seeds in a single capsule of a *Maxillaria* in South Brazil, and found the number 1,756,440. The same plant sometimes produces half-a-dozen capsules.

Number of pollen-grains (p. 355).—I have endeavoured to estimate the number of pollen-grains produced by a single flower of *Orchis mascula.* There are two pollen-masses; in one of these I counted 153 packets of pollen; each packet contains, as far as I could count, by carefully breaking it up under the microscope, nearly 100 compound grains; and each compound grain is formed of four grains. By multiplying these figures together, the product for a single flower is about 120,000 pollen-grains. Now we have seen that in the allied *O. maculata* a single capsule produced about 6,200 seeds; so that there are nearly twenty pollen-grains for each ovule or seed. As a single flower of a *Maxillaria* produced 1,756,000 seeds, it would produce, according to the above ratio, nearly 34 million pollen-grains, each of which, no doubt, includes the elements for the reproduction of every single character in the mature plant!

Enumeration of the Orchideæ *which, as at present known, habitually fertilize themselves* (p. 358).—We have now seen that self-fertilization habitually occurs, in a more or less perfect manner, in one of the species of *Ophrys*, of *Neotinea*, *Gymnadenia*, *Platanthera*, *Epipactis*, *Cephalanthera*, *Neottia*, and in those *Epidendreæ* and in *Dendrobium* which often produce flowers that never expand. No doubt other cases will hereafter be discovered. Self-fertilization seems to be more perfectly secured in *Ophrys apifera* and in *Neotinea intacta* than in the other species. But it deserves especial notice that in all these orchids structures are still present, not in a rudimentary condition, which are manifestly adapted for the transport by insects of the pollen-masses from one flower to another. As I have elsewhere remarked, some plants, both indigenous

and naturalized, rarely or never bear flowers, or, if they do bear flowers, these never produce seed. But no one doubts that it is a general law of nature that phanerogamic plants should produce flowers, and that these flowers should produce seed. When they fail to do this, we believe that such plants would perform their proper functions under different conditions, or that they formerly did so and will do so again. On analogical grounds I believe that the few orchids which do not now intercross, either did formerly intercross (the means for effecting this being still retained) or that they will do so at some future period under different conditions, unless, indeed, they become extinct from the evil effects of long-continued close interbreeding.